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MYCOFLORISTIC IMPRESSIONS OF A EUROPEAN MYCOLOGIST IN AMERICA

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(WITH PLATE 1)

Coming over from Denmark late in the summer of 1931, I made a circuit which took me through the majority of the States and parts of southern Canada. Setting out from New York in the middle of August, my itinerary took me through Massachusetts, Vermont, the Adirondacks, Michigan, Minnesota, part of the territory south of Lake Winnipeg to the Canadian Rockies and the Pacific coast from Vancouver to Los Angeles and back to the southeastern States, returning via Washington to New York towards the end of October.

The trip planned in advance by me with the assistance of American friends aroused so much interest that I not only had an excellent opportunity to botanize in some of the best localities, but was able to visit a number of the leading mycologists at home and in their favorite haunts and take part in mycological " conferenciettas " in several scientific centers for the purpose of paving the way for improved Americo-European collaboration in the study of the agarics.

For the overwhelming hospitality and the genuine interest shown me during this highly profitable expedition I cannot too warmly and sincerely thank my American colleagues and friends. Some of my impressions and observations I shall try to set forth.

When a European botanist makes the acquaintance of the plant-life of Northeastern America he cannot avoid being impressed by

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the similarity of the floras on both sides of the Atlantic. To be sure he encounters leading American genera, such as *Aster* and *Solidago,* represented by hundreds of species, which are only scantily represented in the European flora, and vice versa. But apart from these the flora on the American side consists mainly of two types: the *introduced* species and the *parallel* one (*i.e.,* species which, although not identical with the European ones, are so similar that it often requires a keen and practiced eye to distinguish them).

The *introduced* species, although perhaps not very numerous, play a rather prominent part. They are often very common and, as they mainly inhabit cultivated fields, roadsides, and waste places, are rather conspicuous. When strolling along a country lane one cannot avoid seeing everywhere such plants as *Chenopodium album, Sinapis arvensis, Capsella Bursa-pastoris, Cirsium arvense, Plantago major, Dactylis glomerata, Polygonum aviculare* and *Rumex crispus.*

The *parallel* species are likely to attract the newcomer's interest more strongly. They occur in almost all families, and in many cases they are so close to European species that it is difficult to say whether they ought to be characterized as varieties or should be given specific rank. I shall mention only a few as examples (I put the European parallel in brackets): *Populus tremuloides* (*P. tremula*), *Sambucus canadensis* (*S. nigra*), *Plantago Rugelii* (*P. major*), *Parnassia caroliniana* (*P. palustris*), *Populus virginiana* (*P. nigra*), *Larix americana* (*L. europaea*), *Lepidium virginicum* (*L. ruderale*).

These characteristic floristic facts are of course universally known and thoroughly investigated by botanists from either side of the Atlantic. But what about the fungus-flora?

That certain fungi have a universal distribution is a well known fact. These *cosmopolites* are either native (*e.g.,* many coprophilous fungi, such as *Coprini*) or they are introduced from one continent to another, having become established in their adopted home, sometimes even more fully than in their native land. This is true of numerous parasitic forms, such as the potato-blight (*Phytophthora infestans*), the gooseberry-mildew (*Erysiphe Mors-uvae*), and the hollyhock-rust (*Puccinia Malvacearum*).

On the other hand it is also a well established fact that the flora of any continent besides these cosmopolites comprises an element of endemics: species, and even genera, which are exclusively American or European. In the phanerogamic plant world the overwhelming majority of the species are decided endemics. But what about the mycoflora? Is the main body of the American fungus-flora decidedly "American," or does it consist for a large part of cosmopolitan species which are familiar to the European mycologists from of old, and therefore in common parlance are called "European" species? And finally are the specifically American species mainly *parallels,* or are we more likely to meet with species which represent other types, widely separated from those met with in the Old World? In other words, is the American fungus-flora chiefly characterized by *identity, parallelism,* or *incongruity?*

This is a field of investigation which is as yet very incompletely explored. And what is worse, some of the conclusions are of doubtful value. To be sure certain districts of this realm of fungi are comparatively well known and carefully mapped out. This is true of the *parasitic fungi* and also to a certain extent of the suberous and ligneous Polyporaceae. But when we enter the wide land of the agarics (and other fleshy fungi) we at once feel ourselves in a swampy wilderness, where roads are few and the existing landmarks often mere will-o'-the-wisps.

The reasons for this deplorable state of affairs are not far to seek. A direct comparison of European and American finds is not possible: the perishable fruit-bodies would be unrecognizable before reaching the other side of the Atlantic. Cultivation of the American species in European botanical gardens (or vice versa) for the sake of comparison has hardly been attempted, and will probably in most cases be a very difficult undertaking fraught with disappointments. Dried specimens and those otherwise preserved are in most cases of very limited value, and printed illustrations are entirely inadequate for deciding between parallelism and identity.

To these difficulties must be added the one which arises from the inadequacy of the descriptions. The diagnoses of the classical authors are often so defective that it is very difficult if not en-

tirely impossible to identify the species, and the attempts at identification undertaken by modern authors therefore often give contradictory results. The consequence is that when an American mycologist, who knows the " European " species from descriptions only, faces the problem whether a particular fungus, which he finds in Maine or Michigan, is the one named *Agaricus " X "* by Fries, Berkeley, or Quélet, or something else, he will often be at his wit's end and may count on his buttons to settle the case. And the result may be either that he creates a new species, although his specimens were really identical with a European one, or that he dubs his find with one of the classical names, although in truth it is something absolutely different.

A historic example will serve to illustrate: About 1880 Peck, one of the fathers of American mycology, described a mushroom which he referred to Fries' *Agaricus* (*Psalliota*) *campestris silvicola.* Later on he rightly reached the conclusion that it was more closely related to *A. arvensis* than to *A. campestris,* and he therefore altered the name to *Agaricus* (*Psalliota*) *arvensis* var. *abrupta,* which name he in his latest publications modified to *Agaricus* (*Ps.*) *abruptibulba* Peck, thus creating a " new American species." But the fact is, as even a good photograph will prove, that the Peckian species is the very same as the yellowish-white mushroom so frequently met with in any European fir wood, and which by European authors is called *Psalliota silvicola* (Fries) ex Lange or *Ps. arvensis* ex Ricken.

This will serve to illustrate—and similar cases are probably legion—what extraordinary obstacles must be overcome, what knots must be disentangled before we can acquire adequate knowledge in this field, and form well founded conclusions with regard to the problem whether identity, parallelism or incongruity is the most prominent feature of the fungus-floras of the two continents.

My main purpose in visiting America in 1931 was to get by personal observation a firsthand knowledge of this problem. Partly by what I saw myself, and partly by talking it over with American colleagues, I have reached conclusions which, I think, carry us at least a short step forward through the wilderness. But before entering upon a discussion of my results I will give a brief account of my impressions of the localities visited, as they appear to the eye of a Danish mycologist.

As mentioned above, most of my time was spent in the hilly woodlands of Vermont, the Adirondacks (in the northern part of New York State), the more level country around Ann Arbor (Michigan), the low, pine-clad mountains in the lake district southeast of Lake Winnipeg, the Canadian Rockies (Banff and Lake Louise), Vancouver, and the coast ranges and other mountains of Oregon with their vast virginal woods. When I reached California everything was dried up, and not till the middle of October around Washington, on my way back to New York, did I again encounter a rich mushroom vegetation.

To a Danish field-mycologist, accustomed to comparatively small woods and plantations, which everywhere bear the trace of the forester's activity, where stumps are carefully removed and no sick or dead tree allowed to stand, where in short order and uniformity rule supreme, it is an almost overwhelming experience to wander through an American forest, where all kinds of trees can be met growing together, and where fallen decaying trunks and branches, half-hidden in the ground, are the home of innumerable fungi.

First of all, the difference is in the *age* and *kinds* of trees. While in Denmark a plantation or wood generally is made up of thousands of individual trees of the same species and all of one age (having been planted or sown all at one time), and its ground-vegetation of herbaceous plants as a rule likewise is very uniform, the American forest is often a motley collection of different trees, coniferous and frondose (maybe a score of different species to the acre), and the self-sown progeny of the parent trees sprout up everywhere, older and younger together. Under such conditions the whole wood becomes the home of the entire fungus-flora, while in Denmark most of the species are strictly localized. An example will serve to characterize the difference:

Lactarius deliciosus—the well known edible milksop—here in Denmark is strictly confined to our plantations of *Picea.* But more than that, it is confined to plantations of a certain age (rather young). If anyone has the opportunity to watch the growth and development of such a plantation, he will therefore see *Lactarius deliciosus* make its appearance and in the course of a series of years disappear again, when the trees completely overshadow the ground and quell the grassy vegetation below. But in an Ameri-

can forest no such periodicity is likely to occur; it is not a plantation of a certain age, but a collection of trees of all ages.

The fungus-flora under such conditions is very rich. In good seasons the American woods are a true Eldorado for the mushroom-hunter. This "embarras de richesse" is likely to overpower the botanist from foreign parts. What is particularly bewildering to the Danish field-mycologist is the apparent lack of any intimate relation between certain species of fungi and certain species of trees. Of course even the Danish fungus-flora abounds in species which are to be met with under all and any conditions, in all kinds of woods, such as *Hypholoma fasciculare, Inocybe geophylla,* and *Laccaria laccata.* But a very large number are strictly attached to certain trees, being either fagophilous, pinophilous, laricophilous, or at least confined to coniferous or frondose woods. Thus it cannot escape the attention of a mycologist who studies the Danish flora that, for instance, *Boletus bovinus, Limacium hypothejus, Gomphidius viscidus* and *G. roseus,* are strictly confined to our pine woods, while *Tricholoma psammopodum* and *Boletus elegans* grow under *Larix.* But in an American forest, where all kinds of trees are often crowded together, pinophilous and dryophilous species may be met with on the same spot. No wonder that the American mycologists, when describing the habitat of a certain fungus, often resort to such vague expressions as "in woods," "in shady places," "under trees" and the like, while a careful European mycologist is likely to be more precise in this respect. Still, although more difficult to ascertain, the connection between a fungus and its specific tree can generally be traced even in American woods, at least in those cases where the attachment is absolute.

Altogether such a mycological survey as mine, extended over vast territories, rich on contrasts and extremes, is a unique experience, stimulating and inciting to a more thoroughgoing study of this part of the vegetable kingdom.

PARALLELISM AN IDENTITY OR INCONGRUITY

Returning to the main subject: What then are the conclusions, if any, with regard to the similarity or dissimilarity of the American and European flora of agarics (and other hymenomycetes), to

be gathered from these forays and mycological discussions? Of course even such a ten weeks' trip is by far too short a time for final conclusions. Nevertheless I make bold to state as a preliminary result that the difference between the European and the American fungus-flora is not nearly so great as might be expected from American monographs and floras.

If one turns to such publications, of later years, the general impression will be that the proportion between exclusively American species and "Europeans" is about 7:3. But not only in the eastern States but also in the North and West, wherever I gathered a fairly large number of species, I found more nearly the inverse proportion: 70 per cent which were known to me from the European side of the Atlantic, against 30 per cent specifically American. Wherever a European mycologist may go in American woods he will meet with species familiar to him. Generally the main aspect of the American fungus-flora will be very "European." Or to put it more correctly: *The American mycoflora has more of a cosmopolitan stamp than of an exclusively American one.*

And this main conclusion will hardly be modified to any considerable extent by further and more thoroughgoing investigations. To be sure it is not unlikely that a number of rare species, which do not play a prominent part on the mycological stage and which to a large extent will have escaped my eye, are exclusively American. But on the other hand it is also highly probable that species which are now counted exclusively American will be met with also on the European side of the Atlantic by more careful investigators. In fact recent European publications have brought to light a considerable number of such cases. I myself have found *Pleurotus Rhacodium* (Berk. & Curt.), and *Lactarius griseus* (Peck) has been met with in France. Evidently "the pond" is too narrow to bar out such peregrinating species.

New evidence for the preponderance of the cosmopolitan species over the exclusively American ones is also brought out in a recent work (P. F. Shope: The Polyporaceae of Colorado). Although the climatic conditions and the phanerogamic flora of Colorado are very different from the European type, only 27 per cent of the Polyporaceae enumerated are exclusively American. The fact that most *Polypori* can be identified in a dried condition and their

identity with European species therefore more easily ascertained, will account for this result.

But what about *parallelism* in the world of fungi?—It goes without saying that the more numerous the truly Americo-European species are the less will be the chance of meeting with parallels. Still their number seems to be not at all insignificant. The most prominent and best known of these parallel species is the orange-yellow "fly-mushroom." While in Europe *Amanita muscaria* is almost always bright scarlet (a brown variety is mentioned by Fries but seems to be exceedingly rare), all over the Eastern States a similar species but with a clear orange-yellow hue occurs. This American form also differs slightly from the European one by a faint ochrey tinge of the white dots on the cap (which in the European form are pure white). Whether this American type should be called *A. muscaria* var. *americana* or raised to specific rank is a matter of taste. The existence of this orange-colored American form is the more remarkable because the scarlet European type also occurs in certain parts (*e.g.*, the eastern Canadian provinces and Oregon, where it is said to attain gigantic dimensions).

Also the European *Amanita virosa* has a parallel form *A. bisporigera,* which differs from *A. virosa* by its much smaller dimensions and particularly in its two-spored basidia. It is also very close to *A. verna,* which species—while rare in North Europe—seems to be very common in America (eastern United States), figuring there as a kind of substitute for *A. phalloides,* which seems to be almost unknown in America, while it is very common with us.

Whoever knows the rare species of *Lactarius, L. scrobiculatus* (characterized by the latex quickly changing into chrome-yellow), and in an Adirondack woods finds a *Lactarius* of exactly the same general appearance but with the latex turning lilac instead of yellow, will feel inclined to count it an American parallel, if this lilac-milked form had not been encountered half a century ago in the Bavarian mountains in Germany and named *L. repræsentaneus.* But what a striking example of the wide distribution of a rare species! One of the most remarkable parallels in America, as well in the southern as in the northern states, is *Lactarius de-*

ceptivus, which bears a striking likeness to the European *L. piperatus,* but is easily recognized—when young—by having an almost cottony velum edging the cap.

Also the "edible milksop" *Lactarius deliciosus* (which by the way is rather common in the United States) has an exclusively American parallel, *L. subpurpureus.* The shape of the cap, the size and texture are exactly alike, but the milk of *L. subpurpureus* is dark dingy purple, and the original color of the cap and gills, which changes to dull green with age as in *L. deliciosus,* is a dingy flesh color, while *L. deliciosus* is tile-red with carrot-red latex.

A fungus-foray in America is an excellent training for a mycologist desirous of sharpening his eye for slight differences and minute characteristics. Often the parallel species are so close to each other that anyone not absolutely wide awake will fail to distinguish them. A very characteristic example may be cited: Every European mycologist knows the large *Mycena,* so common in our beech woods, which is called *M. pelianthina* and which is so easily recognized by the blackish-purple edging of the gills. This species is mentioned in several American lists. And to be sure the very first day I botanized in Vermont I encountered a *Mycena* answering almost exactly to the description of *M. pelianthina.* Still it struck me that the color was slightly different; the entire plant, but particularly the stem, had a flush of amber-yellowish, which never occurs in the European *M. pelianthina.* And when further investigation showed that the spores were about 1½ times the size of those of *M. pelianthina,* it was clear to me that the American form would have to receive a specific name (I propose **M. pseudopelianthina** nom. nov.) and represented a case of close parallelism.

Also a *Lepiota* very close to the common European-American species *L. clypeolaria* was collected in the same parts. It differs from the genuine *L. clypeolaria* by being considerably shorter and smaller and—what is more important—by having quite small oval spores ($6 \times 4\,\mu$), while those of *L. clypeolaria* are almost fusiform and about three times as long.

The genus *Pluteus* affords several cases of particular interest. In the Adirondacks I saw a single specimen of the brilliant scarlet species which was named *P. caloceps* by Atkinson. Except for

the bright vermilion color it is in every respect like the European *P. leoninus* and might be taken for an American "parallel"—if the very same scarlet form had not been recorded in Europe (England and Denmark), and figured in Cooke's Illustrations, under the name *P. leoninus* var. *coccineus*. Another possible parallel to *P. leoninus* is a tiny little yellow species called by American mycologists *P. admirabilis*. I have never seen the European *P. leoninus,* which is said to be somewhat larger; but it appears to me rather doubtful whether *P. admirabilis* really deserves specific rank.

The European species *Pholiota erebia* (which even in Europe has been dubbed with a number of names, the most awkward being that of "*Armillaria denigrata*") apparently has a lot of American substitutes. Peck has a long series of names, such as *Pholiota aggericola* and *P. indecens*. But as far as I can see none of these differ materially from the various forms of *Pholiota erebia* occurring on the European side of the Atlantic.

One of the most peculiar cases of parallelism is the existence in America of a phosphorescent form of *Panus stipticus*. While there is no record—as far as I know—of any phosphorescence in the European form, the American one is renowned for its bright noctilucency. I myself encountered this phosphorescent form in North Carolina (Cherokee Co.) in 1927. When seen by daylight the specimens were exactly like those so commonly collected in Denmark. Whether the phosphorescence is a real specific difference or can be accounted for by atmospheric conditions (or bacteria) remains to be decided by further investigations. Finally I may also mention that the genus *Pleurotus* includes an American parallel. *P. Rhacodium* differs from *P. applicatus* only in the black plushy coating on top of the pileus. But this species also has in recent years been found in Europe (Denmark).

Altogether the number of true parallels substituting European forms in the Western hemisphere, and not found on the European side of the Atlantic, seems to be rather limited.

Evidence is as yet far too incomplete to draw any final conclusions with regard to the problem of parallelism. But to my mind the facts point in a certain direction: Everywhere in the vegetable and animal kingdom new "small species" or varieties seem to arise by "*mutation*" (sudden leaps or sidesteps from the straight

path of heredity). If such new forms be equally well or better adapted to the natural conditions in the country where they arise, they may establish themselves there or even become the exclusive possessors of the territory hitherto occupied by the parent species. If such new forms have limited means of dispersal they will become local species. If adapted for wide dispersal, they may gradually spread over unlimited areas.

Supposing such mutations occur among fungi, which are easily dispersed, there is an overwhelming probability that the new species in the course of time will invade adjacent countries, thus reestablishing the temporarily disturbed identity of the floras. And the world wide distribution of a great number of agarics shows that even the Atlantic is too narrow to prevent such migration. Such cases as those mentioned (*Pluteus caloceps, Pleurotus Rhacodium*, and *Lactarius repraesentaneus*) may be explained this way, whether their origin be on this side of the Atlantic or in America. And it is not at all unlikely that such species as *Lactarius subpurpureus* and *Mycena pseudo-pelianthina,* hitherto only known from the Western hemisphere, will in time be discovered also somewhere in the Old World.

By far the greatest distinction in the world of fungi is not between a *western* and an *eastern* flora, but between southern and northern. The distinctive features of the tropical and subtropical mycoflora are very pronounced, subcoriaceous agarics like *Marasmius* and *Lentinus* abound, as well as Phalloids, in the south; and even the southern temperate climates have a flora of their own. In Europe we have a considerable number of Mediterranean species which never (or very rarely) overstep the barrier of the Alps. Other species (such as *Amanita caesarea*) have their northern limit in central Germany, or may extend to northern Germany or southern Denmark (species of truffels, *Amanita solitaria,* etc.). On the other hand certain northern species, which abound from the Rocky Mountains to the Scandinavian subarctic zone, such as *Stropharia depilata,* do not reach so far south as Germany. Similar cases may probably be cited from America.

But in addition to the direct effect of the climatic conditions, the fungus-flora evidently is influenced by the phanerogamic vegetation, more especially by the presence or absence of certain trees to

which the particular species is attached. This may account for a good deal of the incongruity of the floras of Europe and America, and those of the eastern and western United States.

That the American *Agaricus*-flora, in spite of the super-abundance of Americo-European species, comprises a great number of clearly distinct and often very characteristic species, is evident. To a European mycologist it adds a certain zest to the joys of the day in an American wood to meet with such extraordinary types as *Amanita flavoconia, Clitocybe illudens, Laccaria ochropurpurea, Collybia myriadeophylla, Mycena Leajana* and *M. aurantidisca, Volvaria pubescentipes, Clitopilus abortivus, Entoloma salmoneum* and *E. strictius, Pholiota albo-crenulata* and *P. erinacella, Russula compacta, Marasmius siccus* and *M. pulcheripes, Boletinus pictus,* and *Craterellus Cantharellus.*

But stronger and more lasting than any other impression is the evidence of the wonderful cosmopolitanism of the Agarics. When you have once found, in a Danish *Sphagnum*-bog, a few specimens of the " new " species *Stropharia psathyroides* Lange, it gives you a shock to meet with the very same plant in a bog in Oregon, near the Pacific Coast—and only an hour later to come upon *Lepiota cygnea* Lange, of which the only known specimens were hitherto those gathered in 1925, a few miles from my Danish home!

Who can trace the aerial course of the spore?!

THE HYDNACEAE OF IOWA. II. THE GENUS ODONTIA

L. W. Miller

(with plates 2 and 3)

Odontia is the only strictly resupinate genus of the Hydnaceae characterized by the presence of cystidia. *Steccherinum ochraceum, S. lacticolor* and *S. setulosum* have cystidia and may occur resupinate but these can be distinguished generally by their more coriaceous texture and larger size. Cystidia are readily separated from gloeocystidia, setae and conducting organs but often are distinguished with difficulty from the sterile hymenial organs known as paraphyses. Sterile hymenial organs which are readily distinguished from basidia are here treated as cystidia. A cystidium is generally regarded as the specialized end of an undifferentiated hypha and typically has thickened walls, no conspicuous content and is often incrusted with granular material (Overholts, *1929*). It seems unwise arbitrarily to distinguish between the unspecialized hyphae and typical cystidia projecting at the crest of the tooth in many species of *Odontia,* particularly since this character may vary in a given species.

Key to the species of Odontia

1. Cystidia elongated, fusiform or cylindrical, usually strongly incrusted and with thickened walls. .... (2)
1. Cystidia not as above, variable; if greatly elongated either smooth or only slightly incrusted, or sometimes heavily incrusted, thin-walled, and obscured in axial bundles. .... (7)
    2. Cystidia distinctly fusiform. .... (3)
    2. Cystidia long, mostly cylindrical. .... (4)
3. Cystidia sometimes arising from a specialized, septate, incrusted, axial hypha; spores short cylindrical, 3.5–5 × 1.5–2 µ. .... 1. *O. hydnoides.*
3. Cystidia not arising from a specialized hypha; spores oblong, 4.5–5.5 × 3–3.5 µ. .... 2. *O. Queletii.*
    4. Cystidia largely restricted to the apex of the tooth, usually 1–6 occurring in each tooth, septate, smooth, then heavily incrusted; spores mostly 9 × 4–5 µ. .... 6. *O. setigera.*
    4. Cystidia numerous, projecting from the sides and apex, not septate; spores not exceeding 5 × 3 µ. .... (5)

5. Fructification separable, with numerous rhizomorphic strands; teeth short, hispid; spores 3.5–4.5 × 2–3 μ. ....3. *O. fimbriata.*
5. Fructification adnate, without rhizomorphic strands; teeth slender. . . (6)
   6. Ceraceous; hyphae 2–4.5 μ, with few cross-walls; spores 4–5 × 2–3 μ. ....4. *O. ciliolata.*
   6. Floccose, with a fragile, pruinose hymenial surface; hyphae 5–7 μ, with many septa; spores 3–3.5 × 1.75–2.25 μ. ....5. *O. laxa.*
7. Cystidia long, cylindrical, relatively undifferentiated, smooth, in compact or loose terminal tufts; spores long cylindrical. ....(8)
7. Cystidia similar or otherwise; spores spherical to short cylindrical. . (11)
   8. Cystidia agglutinated by a resin-like material into a more or less compact, cylindrical, viscid fascicle; spores 5–7 × 1–1.5 μ. 10. *O. sudans.*
   8. Cystidia in loose tufts, little more than slightly swollen hyphae projecting at the apex of the tooth. ....(9)
9. Subceraceous, whitish; spines conical, minute; basidia 12–18 × 4–5 μ; spores 6–7 × 2–2.5 μ, flattened on one side. ....7. *O. cristulata.*
9. Subfloccose, near cinnamon-buff; spines larger. ....(10)
   10. Basidia 10–20 × 4–5 μ; spores 7–9 × 1.5–2 μ, curved. 8. *O. alutacea.*
   10. Basidia 18–35 × 5–7 μ; spores 7–10 × 3–4 μ; slightly curved. 9. *O. subalbicans.*
11. Cystidia not restricted to the apical portions of the teeth, consisting of subulate, paraphysoid structures or with enlarged or incrusted terminations. ....(12)
11. Cystidia more or less restricted to the apical or outer portion of the teeth. ....(14)
    12. Cystidia incrusted or bearing crystalline material at the ends. (13)
    12. Cystidia subulate, thin-walled, not incrusted, of the same diameter as the basidia, spores 6–8 × 3–4 μ. ....16. *O. crustosa.*
13. Cystidia terminated by a globose enlargement, usually with radiating crystals; spores 4.5–6 × 2.5–3 μ. ....15. *O. bicolor.*
13. Cystidia consisting of constricted hyphal ends which are incrusted for a distance of 8–12 μ; spores 5–6 × 4–5 μ. ....14. *O. arguta.*
    14. Cystidia incrusted, thin-walled and relatively unspecialized, arising singly or in compact bundles at the apical region of the tooth. The incrusted fascicles or individual cystidia are made more or less conspicuous in a KOH solution. ....(15)
    14. Cystidia smooth or occasionally with scattered crystalline material, often in loose terminal tufts. ....(18)
15. Teeth irregular, obtuse, terminating in white, divided tips. ....(16)
15. Teeth entire, uniformly conical or cylindrical, often with pointed tips. (17)
    16. Fructification honey yellow; teeth rigid, strongly hispid at the apex; spores 6–9 × 3.5–5 μ, faint yellow in mass. ....18. *O. livida.*
    16. Fructification cream buff; teeth short, weakly divided into whitish processes; spores 4–6 × 3–3.5 μ. ....17. *O. crustula.*

17. Fructification dark-gray to burnt umber when fresh, cinnamon-buff to fuscous-black in the herbarium; spores 4.5–6 × 2–3 μ. . 19. *O. fusco-atra.*
17. Fructification mustard yellow to tawny, turning purple upon contact with KOH; spores 4.5–6 × 2–3.5 μ. .... 20. *O. uda.*
 18. Fructification soft, floccose, loosely adnate. .... (19)
 18. Fructification crustaceous, subceraceous or ceraceous, adnate. (20)
19. Teeth bristly on the sides and at the apex, 4 mm. or less in length; cystidia 3–9 μ in diameter, numerous, long cylindrical, thick-walled; spores 4–7 × 2.5–4.5 μ. .... 11. *O. barba-jovis.*
19. Teeth with one or more pointed terminal tufts of cystidia, minute; cystidia 2.5–4 μ in diameter, long cylindrical; spores 4–6 × 3–4 μ. 12. *O. stipata.*
 20. Fructification mars yellow to mars brown; teeth coalesced, and strongly fimbriate at the apex; spores 3–4.5 × 1.5–2.5 μ. (*Oxydontia stenodon*).
 20. Cartridge buff to light ochraceous-buff; teeth 1.5 mm. or less in length, variable, subulate, cylindrical or spathulate; spores 4–6 × 2.5–4 μ. .... 13. (*Radulum?*) *spathulatum.*

1. ODONTIA HYDNOIDES (Cooke & Massee) v. Höhn. Akad. Wiss. Wien. Sitzungsber. **118**: 817. 1909. (PLATE 2, FIG. 1.)

Peniophora hydnoides Cooke & Massee, Jour. Linn. Soc. **25**: 154. 1888.

Odontia conspersa Bres. Accad. Sci. Lett. Rovereto III. **3**: 100. 1897.

Peniophora crystallina v. Höhn. & Litsch. Akad. Wiss. Wien. Sitzungsber. **116**: 828. 1907.

Effused, thin, adnate, ceraceous, then farinaceous, white to cinnamon-buff; margin indistinct; teeth 0.5 mm. or less in length, subulate to cylindrical, variable, generally slender and fragile, subdistant, with prominent projecting cystidia at the sides and crests; hyphae 2–3 μ in diameter, indistinct, no clamp connections seen; cystidia 25–70 × 8–14 μ, subulate or fusiform, walls thickened, incrusted, occasionally more or less fascicled about an axial, incrusted and septate cystidium, 8–10 μ in diameter; basidia 8–15 × 3–5 μ, subulate, with 4 sterigmata; spores 3.5–5 × 1.5–2 μ, short cylindrical, slightly depressed on one side, smooth, hyaline.

This species is identified by its extremely thin fructification, slender, fragile spines, characteristic cystidia and the spore characters. It is separated from *Odontia Queletii* by its more slender teeth and smaller, cylindrical spores. The peculiar axial row of large incrusted cells in a single tooth around which the numerous

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subulate or fusiform cystidia are sometimes arranged, is a helpful character. A careful free-hand section or the slight crushing of a spine will reveal this character. Von Höhnel has indicated that this species may at times be nearly devoid of teeth.

This species does not agree with the original description and figures of *Peniophora hydnoides* Cooke & Massee. Von Höhnel (1909), however, has studied the original specimen and reports that it represents the same species as *Odontia conspersa* Bres. and *Peniophora crystallina* v. Höhn. & Litsch. Iowa specimens agree with Bresadola's description of *Odontia conspersa* and are identical with an authentic specimen from Bresadola at The New York Botanical Garden. The synonymy of these two names is quite generally accepted in Europe. Specimens of *Odontia conspersa* from Bourdot and of *Odontia hydnoides* from Litschauer have also been examined.

This fungus is fairly common in Iowa from June to November on decayed wood of coniferous and frondose species. I have seen no report of its previous occurrence in North America. However, I have seen several specimens at The New York Botanical Garden labeled *Odontia glauca* Ell. & Lang. from Louisiana and an undetermined specimen from Minnesota in the mycological herbarium at the University of Iowa.

2. ODONTIA QUELETII Bourd. & Galz. Bull. Soc. Myc. Fr. **30**: 270. 1914. (PLATE 2, FIG. 2.)

Odontia farinacea Quél. Fl. Myc. Fr. 435. 1888.

Fructification ceraceous or subcrustaceous, very thin, not cracking, white to cinnamon-buff; margin absent, not distinct or narrowly limited and fibrillose; teeth scattered or confluent in groups, subulate to short cylindrical, obtuse, fimbriate; hyphae 2.5–5 μ in diameter, with thin walls, fragile, indistinct; cystidia 40–100 × 8–16 μ, with thick walls, incrusted, usually fusiform, occasionally cylindrical or clavate at the crest, numerous, projecting prominently, subimbricated in the teeth; basidia 15–30 × 3.5–5 μ, cylindrical-clavate, spores 4.5–5.5 × 3–3.5 μ, oblong, smooth, hyaline, 1–2 guttulate.

The description of Bourdot and Galzin and in part that of Quélet indicates a crustaceous fructification which cracks upon drying, more crowded spines, smaller cystidia and does not in-

clude guttulate spores. These differences may not be fundamental and since the species is quite distinct otherwise, the determination is probably accurate. Furthermore, an authentic specimen from Bourdot at the Farlow herbarium resembles our Iowa collections externally and microscopically. *Odontia Queletii* and *Odontia hydnoides* are quite sharply distinguished from other *Odontia* species by the numerous, projecting, thick-walled, incrusted and fusiform cystidia and by the small spores. *Odontia Queletii* is separated from the latter by the stouter and less crowded teeth and by the character of the cystidia and spores. The young growing borders of the fructifications spread out as a very thin layer which is almost invisible under the lens. In these areas the cystidia stand out as prominent upright structures.

Collected four times on deciduous wood near Milford, Iowa, in June and July. Apparently not previously reported from the United States.

3. ODONTIA FIMBRIATA Fries, Epicr. 529. 1838. (PLATE 2, FIG. 4.)

Hydnum fimbriatum Pers. ex Fries, Syst. Myc. **1**: 421. 1821.

Mycoleptodon fimbriatum (Fries) Bourd. & Galz. Bull. Soc. Myc. Fr. **30**: 276. 1914.

Gloiodon fimbriatum (Fries) Donk, Ned. Bot. Ver. **1**: 79. 1930.

Entirely resupinate, effused, membranaceous, coriaceous, separable, surface plainly marked by intricately branching, rhizomorphic strands, vinaceous-buff to fawn colored; border fibrillose and rhizomorphic; teeth wart-like, short, hispid at the crest, usually subdistant, more crowded over the rhizomorphic strands; hyphae 2.5–4.5 μ, mostly thick-walled, with few cross-walls and no clamp connections, or thin-walled, indistinct and with occasional clamp connections in the subhymenial region; cystidia 50–80 $\times$ 7–9 μ, clavate-cylindrical, obtuse, thick-walled, incrusted, greatly elongated; basidia 12–20 $\times$ 3–5 μ, clavate, with 4 sterigmata; spores 3.5–4.5 $\times$ 2–3 μ, elliptical, smooth, hyaline.

This species is recognized by its cinnamon color, separable membrane and much branched rhizomorphic strands. The coriaceous texture and the character of the cystidia show similarity to *Steccherinum ochraceum* as indicated by Bourdot and Galzin who

have placed the two species together in the genus *Mycoleptodon*. *O. fimbriata* is a typical *Odontia* except in its coriaceous fructification and this character alone does not seem to be a sufficient reason for placing it in another genus.

Abundant in Iowa. Collected from June to December on frondose species, particularly oak. Reported from central and eastern United States.

4. **Odontia ciliolata** (Berk. & Curt.) comb. nov. (PLATE 2, FIG. 5.)

Hydnum ciliolatum Berk. & Curt. Jour. Bot. & Kew Misc. **1**: 235. 1849.

Effused, ceraceous, thin, adnate, cracking in drying, light ochraceous-buff; border not differentiated or rarely fibrillose; teeth 0.7 mm. or less, slender, crowded, hispid, extending to the margin; hyphae 2–4.5 μ, thick-walled, with few cross walls, or thin-walled and with occasional clamp connections in the subhymenial layer; cystidia $35–60 \times 5–12\ \mu$, subclavate or subulate, obtuse, thick-walled, incrusted; basidia clavate with 4 sterigmata; spores $4–5 \times 2–3\ \mu$, elliptical, smooth, hyaline.

Two specimens of *Hydnum ciliolatum* Berk. & Curt. were examined at The New York Botanical Garden. One was determined by Cooke. The other Banker compared with the type at Kew and marked " identical." Berkeley's original description also indicates the accuracy of their determinations. These and the Iowa specimens seem closely related to *Odontia fimbriata,* and microscopically are practically indistinguishable. However, this species differs in the adnate, ceraceous and lighter colored fructification, the relatively undifferentiated margin and in the character of the teeth.

Two specimens from Iowa were collected in March and in August on much decayed wood of frondose species. Its occurrence is reported from several scattered localities in the eastern United States.

5. **Odontia laxa** sp. nov. (*laxa,* loose). (PLATE 2, FIG. 6.)

Resupinata, tenuis, subadnata, floccosa, ex albida cremea; aculei 0.7 mm., subulati vel cylindracei, gracile; hyphae 5–7 μ, uniformiae, septatae, subhymeniales tenues, non nodoso-septatae; cystidia $40–75 \times 5–10\ \mu$, cylindracea,

incrustata; basidia 7–9 × 3–4 μ; sporae 3–3.5 × 1.7–3.3 μ, ellipsoideae, leves, hyalinae.

Resupinate, very thin and fragile, loosely adnate, soft, floccose. with a pruinose hymenial surface, white to pinkish buff; margin floccose or thin and appressed, sometimes fibrillose, slightly darker in color; teeth subulate to cylindrical, very slender, with prominent cystidia at the sides and the crests; hyphae of the subhymenial region and in the axial portions of the teeth 5–7 μ in diameter, uniform, thick-walled, septate, branching at wide angles, without clamp connections, hyaline or slightly yellowish and often incrusted, becoming more compact, smaller, hyaline, thin-walled and sometimes obscured by granular material in a thin hymenial layer; cystidia 40–75 × 5–10 μ, numerous, consisting of the cylindrical ends of the coarse hyphae in the axial portion of the tooth, projecting, strongly incrusted; basidia 7–9 × 3–4 μ, indistinct; spores 3–3.5 × 1.75–2.25 μ, ellipsoid, attenuate, hyaline.

A specimen labeled *Hydnum fascicularia* Berk. & Curt., on elm, July 30, 1893, in the Morgan collection in the mycological herbarium of the State University of Iowa and presumably from Ohio is identical with Iowa material. A portion of the Morgan specimen was compared with the type of *Hydnum fascicularia* at Kew by Miss Wakefield who reports that it is certainly not the same. Since the Morgan collection is considerably larger than the single Iowa specimen it is here designated the type of *Odontia laxa.* This species has cystidia similar to those in *O. fimbriata* and *O. ciliolata* but is readily distinguished by the floccose texture, the large, uniform hyphae and the smaller spores.

Apparently rare in Iowa. On a fragment of bark near Wellman, Iowa. October.

6. **Odontia setigera** (Fries) comb. nov. (PLATE 2, FIG. 3.)

Thelephora setigera Fries, Elench. Fung. **1**: 208. 1828.

Kneiffia setigera Fries, Epicr. 529. 1838.

Corticium myxosporum Karst. Medd. Soc. Faun. Fl. Fenn. **9**: 53. 1882.

Odontia acerina Peck, Ann. Rep. N. Y. State Mus. **53**: 847. 1900.

Peniophora setigera (Fries) v. Höhn. & Litsch. Ann. Myc. **4**: 289. 1906.

Fructification resupinate, effused, adnate, at first thin, arachnoid under the lens, then thickened, subfloccose to subceraceous, sometimes cracking, white to pinkish buff; margin similar, white; teeth short, conical, blunt, weakly hispid at the apex; hyphae 2–5 μ in diameter, with numerous clamp connections, loosely arranged; cystidia 25–75 $\times$ 6–11 μ, cylindrical, sometimes tapering, septate, with clamp connections, projecting prominently near the apex of the teeth, at first naked, becoming incrusted with coarse oxalate crystals; basidia 15–35 $\times$ 5–8 μ, clavate, with 4 sterigmata; spores 6–12 $\times$ 3.5–6 μ, mostly 9 $\times$ 4–5 μ, ellipsoid to cylindrical, smooth, hyaline, often guttulate.

This species is generally referred to *Peniophora* in Europe. Smooth forms have been reported, but these are apparently unusual. A more or less distinct papillose or warty hymenium is present in our many Iowa specimens and in the dozens of specimens from Europe and North America, which I have examined at The New York Botanical Garden and at the Farlow herbarium. The odontoid character of the fructification is also shown by the usual position of the cystidia at or near the apex of the warts. A cross-section through a tooth of *Odontia granulata*[1] (= *O. setigera*) with a single cystidium is shown by Overholts (1929) on plate 2, figure 5. In forms with less pronounced warts the cystidia appear more scattered but this is not unusual in other species of *Odontia*. If the present distinctions between *Peniophora* and *Odontia* are to be maintained this species seems clearly to belong to the latter genus.

Odontia setigera may be distinguished from *O. cristulata* by the larger, more conspicuous and less fascicled cystidia and by the characteristic spores.

Very abundant in Iowa on wood or bark of oak and many other frondose and coniferous species. Collected from June to December. Reported from various localities in the central and eastern portions of the United States.

7. ODONTIA CRISTULATA Fries, Epicr. 529. 1838. (PLATE 2, FIG. 10.)

Effused, thin, soft subceraceous, slightly cracking and pruinose, adnate, white to cream color; margin whitish, floccose or pruinose;

[1] *Odontia granulata* is a name suggested by Burt but apparently never published. References have been made to it in literature by Lloyd and Overholts. It is *O. setigera* as here understood.

teeth subdistant, conical, very short and fragile, fimbriate at the crest; hyphae 2.5–5 μ in diameter, loosely interwoven, dividing upward and becoming quite compact in the hymenium, with numerous clamp connections; cystidia only slightly differentiated, often irregular in shape, loosely fascicled at the apex of the teeth, with spherical clusters of crystals, with or without cross-walls; basidia 12–18 × 4–5 μ, clavate, with 2–4 sterigmata; spores 6–7 × 2–2.5 μ, cylindrical, flattened on one side, smooth, hyaline, often 1–2 guttulate.

Bresadola and Bourdot and Galzin give the spore size as 8–10 × 3.5–4 μ. However, a specimen of *O. cristulata* Fries from Bourdot at the Farlow herbarium resembled the Iowa specimen externally and seemed to be identical in microscopic structure. This species closely resembles *O. setigera* in external appearance but has less conspicuous cystidia and apparently smaller spores.

Collected only once on much decayed deciduous wood in November at North Liberty, Iowa. No record of its previous occurrence in the United tates has come to my attention.

8. ODONTIA ALUTACEA (Fries) Bourd. & Galz. Hym. Fr. 422. 1927. *non* Bres. (PLATE 2, FIG. 9.)

Hydnum alutaceum Fries, Syst. Myc. **1**: 417. 1821.

Kneiffia stenospora Karst. Hedwigia **25**: 231. 1886.

Resupinate, effused, adnate, thin, loose and floccose, near cinnamon-buff; margin similar; teeth scattered or crowded, conical, pointed or slightly fimbriate; hyphae 2.5–5 μ in diameter, thick-walled, clamp connections numerous; cystidia in terminal tufts and widely scattered along the sides, little differentiated, not incrusted, with or without cross-walls, obtuse; basidia 10–20 × 4–5 μ, with 4 sterigmata; spores 7–9 × 1.5–2 μ, cylindrical, curved, smooth, hyaline.

Bresadola (1897) and probably also Quélet (1888) applied the name *Odontia alutacea* (Fries) to a form of *Odontia arguta* (Fries) Quél. Bourdot and Galzin (1927) report receiving a fragment of an authentic specimen of *Hydnum alutaceum* Fries from Romell. They therefore base their conception of the species on this specimen. My specimen agrees entirely with their description and with an authentic specimen of *Kneiffia stenospora* from Karsten at The New York Botanical Garden, which Bourdot and Galzin cite as a synonym. Three specimens of *O. alutacea* re-

ceived from Litschauer also agree closely with our Iowa collection. The floccose texture and long, cylindrical spores are very characteristic.

One specimen on oak was collected in Iowa, September, 1931. Bourdot and Galzin report a specimen from Lloyd (n. *09130*) but do not state that it was collected in the United States. It is doubtful whether the other records of *Hydnum* (*Odontia*) *alutaceum* Fries in the United States refer to the same species as here defined.

9. ODONTIA SUBALBICANS Pers. ex Bres. Ann. Myc. **1**: 87. 1903. (PLATE 2, FIG. 8.)

Hydnum granulosum var. *albicans* Pers. Myc. Eu. **2**: 184. 1825.

Effused, floccose, with a thin subceraceous hymenium which is easily crumbled when dry, loosely adherent, light pinkish cinnamon to cinnamon-buff; border similar or floccose, thinning out; teeth short, somewhat crowded, with pointed and fimbriate apex; hyphae 2.5–6 μ in diameter, with numerous clamp connections, loosely arranged next to the substratum and compact in the hymenium; cystidia 4–6 μ in diameter, little differentiated, axial or terminal, fascicled, projecting, septate and with clamp connections; basidia 18–35 $\times$ 5–7 μ, clavate, with 2–4 sterigmata; spores 7–10 $\times$ 3–4 μ, cylindrical, slightly curved, smooth, hyaline, granular or guttulate.

This species is recognized by its relatively large cylindrical spores and by the slender fascicles of projecting hyphae at the apices of the teeth. Bourdot and Galzin give the spore size as 7–8.5 $\times$ 2.75–3 μ. The measurement here given, however, is in accord with Bresadola's description. An authentic specimen at The New York Botanical Garden determined by Bresadola is like our Iowa specimens.

Two specimens were collected on much decayed oak wood near McGregor, Iowa, in August. This seems to be the first record of the occurrence of this species in North America.

10. ODONTIA SUDANS (Fries) Bres. Accad. Sci. Lett. Rovereto III. **3**: 100. 1897. (PLATE 2, FIG. 7.)

Hydnum Agardhii Fries, Syst. Myc. **1**: 418. 1821.

Hydnum sudans Alb. & Schw. ex Fries, Syst. Myc. **1**: 425. 1821.

Thelebolus sudans Fries, Elench. Fung. **2**: 51. 1828.

Grandinia Agardhii Fries, Epicr. 528. 1838.

Dacryobolus sudans Fries, Summa Veg. Scand. 404. 1849.

Porothelium Stevensoni Berk. & Br. Ann. Mag. Nat. Hist. V. **1**: 23. 1878.

Porothelium confusum Berk. & Br. Ann. Mag. Nat. Hist. V. **1**: 24. 1878.

Grandinia exsudans Karst. Medd. Soc. Faun. Fl. Fenn. **9**: 51. 1882.

Grandinia sudans Lloyd, Myc. Notes **52**: 741. 1917.

Effused, membranaceous-ceraceous, separable in small pieces, warm buff to cinnamon-buff; margin similar, byssoid or pruinose, sometimes whitish; teeth short, scattered conical or short cylindrical, terminated by a viscid and more or less transparent, cylindrical or tapering, and projecting fascicle of cystidia; hyphae 1–3 μ in diameter, thin-walled, somewhat indistinct; cystidia 3.5–5 μ in diameter, walls thickened, septate, agglutinated and projecting as a prominent fascicle; basidia 15–24 $\times$ 3–4 μ, cylindrical-clavate, with 4 sterigmata; spores 5–7 $\times$ 1–1.5 μ, cylindrical, curved, smooth, hyaline.

The viscid bundles of cystidia are usually very conspicuous under a lens. Their contraction in drying and their more or less transparent appearance have been the cause of several striking errors in literature, as is evident by the rather extended synonymy. The teeth are often described as cupped or excavated, even by comparatively recent authors. This seems never to be true in fresh material. (Lohwag. Ann. Myc. 1931.) Fries in his Systema Mycologicum described the species under the name *Hydnum Agardhii* and apparently regarded *H. sudans* Alb. & Schw. as representing a doubtful species.

O. sudans is fairly common in Iowa. Collected from June to October on wood of deciduous and coniferous species. In Europe this species is reported on coniferous wood only. I have seen no report of its previous occurrence in the United States.

11. ODONTIA BARBA-JOVIS Fries, Epicr. 528. 1838. (PLATE 3, FIG. 1.)

Hydnum Barba-Jovis With. ex Fries, Syst. Myc. **1**: 421. 1821.

Hydnum Nyssa Berk. & Curt. Grevillea **1**: 100. 1873.

Kneiffia irpicoides Karst. Bidr. Finl. Nat. Folk **48**: 368. 1889

Widely effused, soft floccose, loosely adnate, whitish to pinkish buff or slightly darker; teeth variable in size, not exceeding 4 mm. in length, soft, crowded, slender, blunt or subulate, fimbriate or terminated by one or more tapering tufts of cystidia, also bristly on the sides; hyphae 2–4 μ in diameter, thin-walled or thickened, with clamp connections; cystidia greatly elongated, 3–9 μ in diameter, cylindrical, thick-walled, becoming thin-walled and sometimes incrusted near the outer extremities, projecting in tufts at the apex of the teeth and singly on the sides; basidia 15–25 × 3–6 μ; spores 4–7 × 2.5–4.5 μ, oblong, smooth, hyaline, often 1-guttulate.

One specimen which I am referring tentatively to *Odontia Barba-jovis* is similar to *Odontia stipata* but differs in the more bristly teeth, the thick-walled, often capitate and more conspicuous cystidia and the smaller spores. The spore size is 4–5.5 × 2.25–3 μ, which is slightly less than reported by various European writers. This specimen differs also from material determined as *O. Barba-jovis* by Bresadola and Bourdot at The New York Botanical Garden in the smaller teeth and cystidia, some of which are incrusted at the outer extremities or bear a glistening and somewhat amorphous covering over the tips. Bourdot and Galzin (1927) describe a form with terminally incrusted cystidia. Two other Iowa specimens agree closely with the European conception of *Odontia Barba-jovis*. An authentic specimen of *Kneiffia irpicoides* Karsten and a fragment of the type of *Hydnum Nyssa* Berk. and Curt. at The New York Botanical Garden were also examined and seem clearly to be the same species.

Collected in October on deciduous wood near North Liberty, Iowa. Reported from several scattered localities in the eastern United States.

12. ODONTIA STIPATA (Fries) Quél. Fl. Myc. Fr. 435. 1888. (PLATE 3, FIG. 2.)

Hydnum stipatum Fries, Syst. Myc. **1**: 425. 1821.

Resupinate, effused, thin, soft floccose, loosely adnate, whitish becoming light buff; margin white, tomentose, sterile; teeth slender, entire or divided, pointed or sometimes slightly fimbriate, unequal in length; hyphae 2–3.5 μ, thin-walled to thick-walled, with clamp connections; cystidia 2.5–4 μ in diameter, emerging in terminal tufts, not strongly differentiated; basidia 12–20 × 3–5 μ, clavate to cylindrical, with 4 sterigmata; spores 4–6 × 3–4 μ, oblong, smooth, hyaline.

Odontia stipata is characterized by its very soft, floccose fructification, the pointed teeth and the emerging tufts of cystidia. The Iowa material closely resembles European specimens determined by Bourdot, Bresadola and Litschauer. It differs, however, from a waxy specimen in the Ellis collection at The New York Botanical Garden apparently determined by Bresadola, but this was clearly another species.

Collected once on decorticated elm log near Wellman, Iowa, in October. Reported from eastern United States. The Iowa specimen referred to *O. stipata* (Fries) Quélet by Cejp (1931) is *Radulum spathulatum* (Fries) Bres. as here understood.

13. (RADULUM ?) SPATHULATUM (Fries) Bres. Ann. Myc. **1**: 89. 1903. (PLATE 3, FIG. 3.)

Hydnum spathulatum Schrad. ex Fries, Syst. Myc. **1**: 423. 1821.

Irpex spathulatus Fries, Elench. Fung. **1**: 146. 1828.

Effused, thin, soft, ceraceous or sometimes with a sub-ceraceous hymenial layer and floccose next to the substratum, often cracking in drying, cartridge buff to light ochraceous-buff; border similar or floccose and white; teeth 1.5 mm. or less in length, variable, subulate to cylindrical or spathulate to irpiciform, obtuse or pointed fimbriate or with pointed processes projecting from the sides and crests; hyphae 2–3 μ in diameter, with clamp connections, occasionally incrusted; cystidia not distinct, largely undifferentiated hyphae projecting from the hymenium or in bundles from the side and crest of the tooth; basidia $12–16 \times 3.5–5\ \mu$, clavate, with 2–4 sterigmata; spores $4–6 \times 2.5–4\ \mu$, subspherical to elliptical, smooth, hyaline, sometimes 1-guttulate.

This species is quite variable and lacks distinct diagnostic characters. It resembles *Odontia arguta* and is considered a form of this species by Miss Wakefield. However, the smoother and more compact, ceraceous fructification and the absence of the conspicuous, incrusted cystidia, seem clearly to separate the two forms. Litschauer referred several Iowa specimens of this species to *Radulum spathulatum* (Schrad.) Bres. He reports having had many specimens so determined for him by Bresadola and sent me a number of European specimens, including an authentic one from Bresadola. Whether Bresadola's conception is correct is not known. It does not seem to belong in the genus *Radulum*. The

frequently flattened and irregular teeth suggest characters of *Irpex,* but its general aspect and microscopic detail is too near *Odontia.*

Common in Iowa from early June to October, on wood of frondose and coniferous species. Collected throughout the year. Many specimens variously determined from the central and eastern United States were seen at The New York Botanical Garden and in other herbaria. A number of these were referred to *Hydnum pallidum* Cooke & Ellis.

14. ODONTIA ARGUTA (Fries) Quél. Fl. Myc. Fr. 435. 1888. (PLATE 3, FIG. 4.)

Hydnum argutum Fries, Syst. Myc. **1**: 424. 1821.

Odontia alutacea Bres. Atti Accad. Rovereto III. **3**: 97. 1897.

Effused, thin, soft, floccose, appearing pubescent, pruinose when dry, cartridge buff to cinnamon-buff; margin similar, thinning out or floccose; teeth 1–2 mm. in length, variable, at first short, then cylindrical or subulate, pointed, divided or penicillate at the apex, finely pubescent; hyphae 2–4 μ in diameter, distinct, with clamp connections; cystidia mostly $20–35 \times 3–4\ \mu$, fusiform or subulate, with incrusted terminations projecting from the hymenium, sometimes accompanied by others which are 4–6 μ in diameter, cylindrical, with obtuse or slightly enlarged, smooth or incrusted terminations, and up to 9 μ in diameter; basidia $10–16 \times 4–5\ \mu$, clavate, with 4 sterigmata; spores $5–6 \times 4–5\ \mu$, obovate, smooth, white, sometimes 1-guttulate.

This species resembles *Radulum spathulatum* (Fries) Bres. It can be distinguished readily by the variable but characteristic cystidia, the more floccose texture, and the pubescent appearance of the surface of the fructification. The hymenial cystidia with incrusted terminations separate it readily from other related species of *Odontia.* The fructifications are often so thin as to appear arachnoid under the lens.

O. arguta is abundant in Iowa on old wood of deciduous and coniferous species throughout the year. It was reported previously from Iowa by Cejp (1931) but this report is based on a species tentatively referred in this paper to *Radulum spathulatum* (Fries) Bres. Its distribution in North America cannot be determined from published notes. Dozens of herbarium specimens from many localities throughout central and eastern North Amer-

ica have been examined. Many of these were undetermined or referred to various names.

European specimens of *O. arguta* and descriptions by recent European writers indicate that our North American forms are identical. An authentic specimen of *Odontia alutacea* Bres. was examined at The New York Botanical Garden. *Hydnum caryophylleum* Berk. & Curt. seems to be a closely allied species.

15. ODONTIA BICOLOR (Fries) Bres. Ann. Myc. **1**: 87. 1903. (PLATE 3, FIG. 5.)

Hydnum bicolor Alb. & Schw. ex Fries, Syst. Myc. **1**: 417. 1821.

Hydnum subtile Fries, Syst. Myc. **1**: 425. 1821.

Odontia subtilis Quél. Fl. Myc. Fr. 435. 1888.

Hydnum serratum Peck, Ann. Rep. N. Y. State Mus. **50**: 112. 1897.

Hydnum echinosporum Vel. České houby. 745. 1922. (Fide Cejp.)

Widely effused, thin, adnate, soft, pruinose, becoming ceraceous in older portions, cracking slightly in the ceraceous portions, cartridge buff when fresh; margin pruinose, indeterminate, often quite wide, concolor or white; teeth up to 0.3 mm. in length, short, fragile, more or less regular in shape, obtuse or divided into several points, scattered evenly, more crowded in the older portions, crests when pointed usually composed of sterile hyphal ends; hyphae 2–3 μ in diameter, thin, collapsed and loosely agglutinated which somewhat obscures the hyphal characters, no clamp connections seen; cystidia 6–18 μ in diameter, terminating in a globose enlargement, covered with radiating crystals or sometimes containing a yellowish material, submerged or projecting; basidia 10–20 $\times$ 3–5 μ, clavate, with 4 sterigmata; spores 4.5–6 $\times$ 2.5–3 μ, oblong, obliquely attenuate, smooth, hyaline.

This species is easily recognized by its characteristic cystidia. The enlarged terminations of the smooth cystidia in many cases are collapsed and apparently empty. These differ from the cystidia in which the enlarged ends are covered with crystals by the fact that they are fewer in number or absent and arise from hyphae of greater diameter.

Collected once in Iowa on a prostrate poplar log in April. Specimens from New York, Michigan, Ohio, Louisiana, Florida,

Georgia and South Carolina also have been examined. These are identical with European specimens determined by Bourdot and by Litschauer. Morgan (1887) referred this species to *Hydnum nudum* Berk. & Curt. The specimens from Florida, Georgia and South Carolina were referred to *Grandinia granulosa* Fries. A fragment of an authentic specimen of *Hydnum subtile* Fries at The New York Botanical Garden and the type of *Hydnum serratum* Peck at Albany were studied.

16. ODONTIA CRUSTOSA (Fries) Quél. Fl. Myc. Fr. 436. 1888. (PLATE 3, FIG. 6.)

Hydnum crustosum Pers. ex Fries, Syst. Myc. **1**: 419. 1821.
Grandinia crustosa Fries, Epicr. 528. 1838.

Fructification resupinate, effused, often orbicular, ceraceous-crustaceous, usually cracked when dry, pinkish buff to cinnamon-buff, sometimes more yellowish; margin pruinose or narrowly floccose, white; teeth small, subulate to short cylindrical, obtuse, sometimes weakly divided into several processes each of which is terminated by a slightly projecting bundle of sterile hyphae, scattered or crowded; hyphae 2–4 μ, with clamp connections, 3–5 μ at the apex of teeth; cystidia fusiform or subulate, few to numerous in the hymenium, barely emerging, of the same diameter as the basidia, thin-walled; basidia 15–30 $\times$ 4–6 μ, with 4 sterigmata; spores 6–8 $\times$ 3–4 μ, subcylindrical, smooth, hyaline, occasionally 1-guttulate.

The subulate, hymenial cystidia are differentiated chiefly by their shape and might well be regarded as paraphyses. This species may be separated from *Odontia crustula* by the subulate hymenial structures and the slightly larger spores. Two specimens at The New York Botanical Garden determined by Bresadola, represent the species as here understood. Three specimens determined by Litschauer have also been studied and appear to be identical. Several specimens of *Odontia crustosa* from Iowa were verified by Litschauer.

Common in Iowa on oak and other deciduous species; collected from April to December. Most of the many specimens from North America referred to this species at The New York Botanical Garden clearly represent other species.

17. **Odontia crustula** sp. nov. (*crustula,* a little crust). (PLATE 3, FIG. 7.)

Effusa, tenuis, crustaceo-ceracea, adnata, paulo secedens, cremea; verrucae breves, conicae vel breviter cylindraceae, obtusae, incisae, apicibus albidis; hyphae 2.5–6 μ, nodoso-septatae; cystidia 4–6 μ diam., cylindracea, fasciculata, adglutinata, incrustata, paulo exserta; sporae 4–6 × 3–3.5 μ, ellipsoideae, leves, hyalinae.

Widely effused, thin, crustaceous-ceraceous, adnate, slightly cracking, cream buff; margin indeterminate, pruinose, or minutely and narrowly floccose, sometimes slightly fimbriate and rhizomorphic, white; warts short, conical to short cylindrical, very obtuse, usually with the crests divided into whitish processes; hyphae 2.5–5 μ in diameter, thin-walled, clamp connections present, incrusted in the axial portion of the tooth; cystidia 4–6 μ in diameter, cylindrical, in heavily incrusted, more or less agglutinated bundles, projecting 15–100 μ at the apex of the tooth; basidia 15–25 × 4.5–7 μ, clavate; spores 4–6 × 3–3.5 μ, ellipsoid, smooth, hyaline or granular, sometimes guttulate.

This species is ceraceous and is characterized by one or more bundles of incrusted and relatively unspecialized cystidia at the crest of the teeth, as is common in many of the species of *Odontia.* However, I have been unable to refer it to any known species. Litschauer reports that he knows no European species to which it may be referred. *Odontia crustosa,* which externally resembles this species, has slightly larger spores and subulate, hymenial cystidia.

Fairly common in Iowa on decorticated wood and bark of deciduous and coniferous species. Collected from June to October. Type specimen collected near Milford, Iowa, on linden, June 16, 1931, by L. W. Miller, and deposited in the mycological herbarium of the State University of Iowa.

18. ODONTIA LIVIDA Bres. Nuovo Giorn. Bot. Ital. **23**: 158. 1891. (PLATE 3, FIG. 8.)

Resupinate, widely effused, ceraceous-crustaceous, cracked, typically honey-yellow but varying from chamois to clay color; margin not differentiated, or whitish, fimbriate; teeth deformed, short rigid, hispid at the apex; hyphae 2–6 μ in diameter, without clamp connections; cystidia 4–8 μ in diameter, cylindrical, elongated, usually heavily incrusted and occurring in compact, branching fascicles which project 25–250 μ at the apex of the teeth; basidia 18–32 ×

5–7 μ, elliptical, smooth, with granular content, sometimes 1-guttulate, faint yellow in mass.

The honey-yellow color, the rigid and hispid spines and the large spores are characters which distinguish this species. An authentic specimen from Bresadola at The New York Botanical Garden has been studied. It is quite like our Iowa specimens. The descriptions of *Odontia corrugata* (Fries) Bourd. & Galz. and *Odontia junquillea* Quél. indicate a very similar fungus.

On linden and oak wood from April to August; fairly common in Iowa. I have seen no previous record of its occurrence in the United States.

19. ODONTIA FUSCO-ATRA (Fries) Bres. Atti Accad. Rovereto III. **3**: 95. 1897. (PLATE 3, FIG. 10.)

Hydnum fusco-atrum Fries, Syst. Myc. **1**: 416. 1821.

Hydnum carbonarium Peck, Ann. Rep. N. Y. State Mus. **40**: 55. 1887.

Odontia membranacea (Fries) Bres. Atti Accad. Rovereto III. **3**: 95. 1897.

Acia fusco-atra (Fries) Pat. Tax. Hymén. 69. 1900.

Acia membranacea (Fries) Bourd. & Galz. Bull. Soc. Myc. Fr. **30**: 258. 1914.

Effused, soft ceraceous, adherent, color variable, dark-gray or fawn color to burnt umber when fresh, cinnamon-buff to fuscous-black in the herbarium; margin pruinose or radially fibrillose, usually lighter in color, sometimes not differentiated; teeth 0.5–2 mm. in length, stout, subulate, mostly entire and pointed or slightly divided at the crest, sometimes ciliate, often remaining pale at the apex; hyphae 3–4 μ in diameter, distinct, with clamp connections, parallel and compact in the teeth, incrusted singly or in fascicles in the axial portion, crystals minute; cystidia 4–5 μ in diameter, cylindrical, incrusted, elongated, arising from the axial portion of the teeth, sometimes a few inconspicuous, thin-walled, subulate, hymenial cystidia are also present; basidia 15–25 × 3–5 μ; spores 4.5–6 × 2–3 μ, short cylindrical, barely depressed on one side, smooth, hyaline.

O. fusco-atra resembles *O. uda* in structure but is readily separated by its dark color. The hyphae are generally larger, more distinct and with more numerous clamp connections. The incrusted hyphae and cystidia are less fascicled.

This species varies considerably in color. The lighter forms tend to have a more distinct margin and are colored slightly in KOH solution. *Hydnum carbonarium* Peck is based on such forms. A specimen of *Odontia membranacea* (Fries) from Bresadola and one from France (Galzin) at The New York Botanical Garden seem to be identical with light colored forms which I am here including in *O. fusco-atra.* Specimens of *Odontia fusco-atra* from Bourdot and from Bresadola were also studied. According to Bresadola *O. membranacea* differs from *O. fusco-atra* in the more slender and crowded teeth and in the slight difference in the color of the initial growth. These differences noted by Bresadola and observed in the specimens which I have studied seem to be due to variation only. The two forms merge and are identical in microscopic characters.

O. fusco-atra is fairly common in Iowa from March to late in November; collected on wood of various frondose species. Previously reported from scattered localities in the eastern United States.

20. ODONTIA UDA (Fries) Bres. Atti Accad. Rovereto III. **3**: 97. 1897. (PLATE 3, FIG. 9.)

Hydnum udum Fries, Syst. Myc. **1**: 422. 1821.

Acia uda Bourd. & Galz. Bull. Soc. Myc. Fr. **30**: 255. 1914.

Effused, soft ceraceous, adherent, mustard yellow to chamois or tawny; margin radially fibrillose or pruinose, sometimes subhyaline; teeth usually crowded, slender, subulate, entire or fimbriate and divided at the crest, apex often white after drying; hyphae 2–4 μ, thin-walled, with rare clamp connections, compact, incrusted in the axial portion of the tooth; cystidia 2–5 μ in diameter, cylindrical, only slightly differentiated, usually emerging in incrusted fascicles; basidia 15–25 $\times$ 3.5–5 μ, clavate, with 4 sterigmata; spores 4.5–6 $\times$ 2–3.5 μ, ellipsoid, slightly depressed on one side, smooth, granular or hyaline.

The fructification turns purple upon contact with a KOH solution. This is often a useful taxonomic character. The fascicles of incrusted cystidia in the teeth usually stand out prominently upon adding KOH. Our specimens agree closely with European material determined by Bourdot, Bresadola and Litschauer.

Common in Iowa on wood of frondose species from March to October, and apparently occurring in the central and the eastern United States. This species was previously reported from Iowa by Cejp (1931).

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EXPLANATION OF PLATES

All figures drawn with the camera lucida. The longitudinal section of a tooth in figure 8, plate 3 at an initial magnification of 175 diameters, reduced to $\times$ 106 in reproduction; all others at an initial magnification of 1650 and reduced to $\times$ 1000.

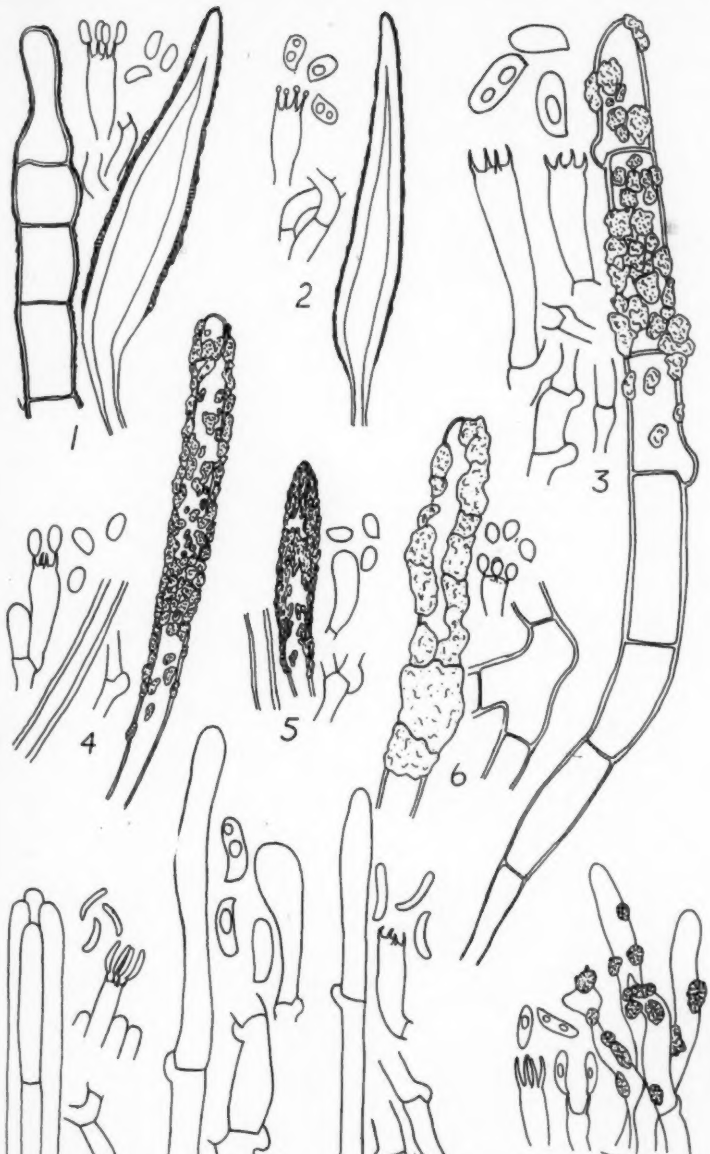
Cystidia or at least their terminal portion, hyphae, basidia and spores are shown in each figure.

PLATE 2

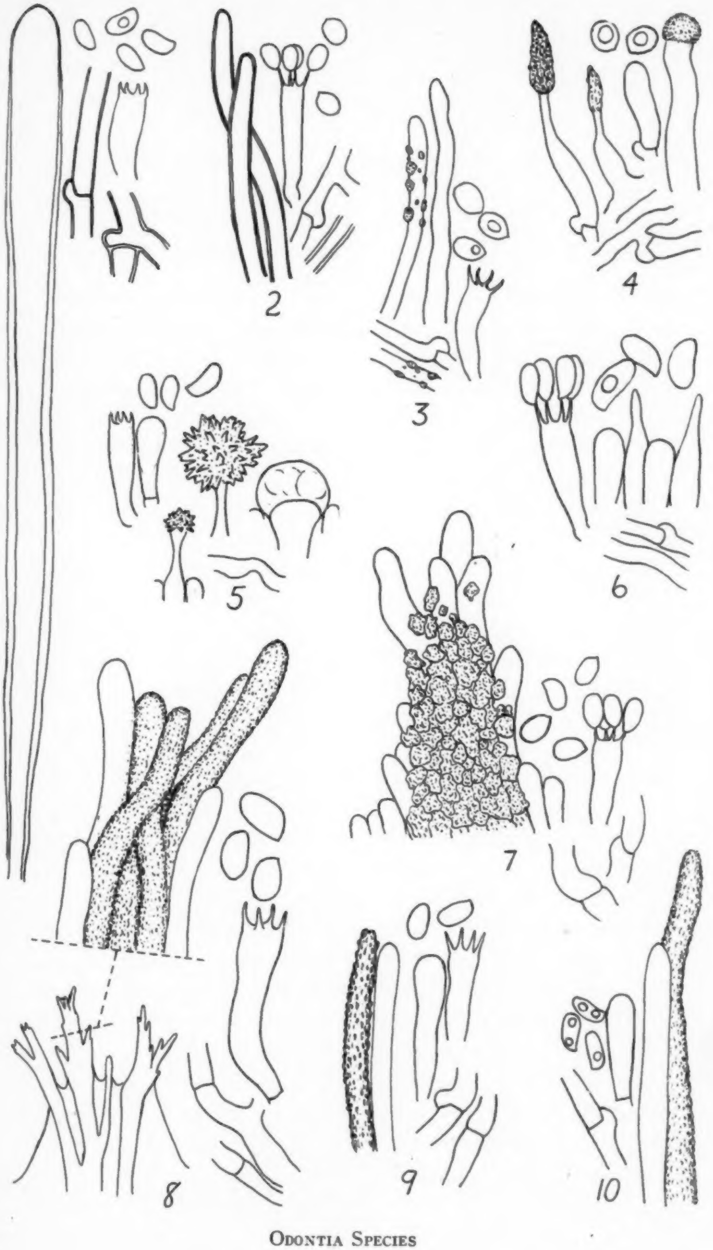
Fig. 1, *O. hydnoides;* 2, *O. Queletii;* 3, *O. setigera;* 4, *O. fimbriata;* 5, *O. ciliolata;* 6, *O. laxa;* 7, *O. sudans;* 8, *O. subalbicans;* 9, *O. alutacea;* 10, *O. cristulata.*

PLATE 3

Fig. 1, *O. barba-jovis;* 2, *O. stipata;* 3, (*Radulum ?*) *spathulatum;* 4, *O. arguta;* 5, *O. bicolor;* 6, *O. crustosa;* 7, *O. crustula;* 8, *O. livida;* 9, *O. uda;* 10, *O. fusco-atra.*



ODONTIA SPECIES



ODONTIA SPECIES

A NEW SPECIES OF HELICOCEPHALUM

Charles Drechsler

(with plate 4)

The genus *Helicocephalum* was erected by Thaxter[1] in 1891 to make provision for a fungus that he found in a laboratory culture on carrion, and accordingly described under the appropriate binomial *H. sarcophilum.* In the brief discussion close resemblance to a large *Mortierella* or *Syncephalis* was pointed out, the similarity obviously applying more especially to the scattered distribution of the plant on the substratum, to the small diameter and aseptate or rarely septate condition of the vegetative hyphae, to the pronounced differentiation of the simple erect sporiferous hypha, and to the presence on the latter of rhizoid-like supporting basal attachments. Features distinguishing the fungus from any of the known genera of Mucoraceae were recognized in the character of the unusually large brown spores, as well as in their development through maturation of segments resulting from the insertion of septa at intervals in the helicoid distended terminal portion of the fertile hypha.

Although more than four decades have elapsed since the appearance of Thaxter's publication, the mycological literature of the intervening period would seem to offer no record of any encounter at first hand either with *Helicocephalum sarcophilum* or with any form sufficiently similar to be recognized as a congener. It may therefore not be unprofitable to set forth the main characteristics of such a congeneric form that made its appearance early in 1933 on rather old maize-meal agar plate cultures originally planted with decaying rootlets. On the mycelia of various species of *Pythium* that first extended themselves through the substratum had become superimposed a mixture of plant and animal life including an abundance of bacteria, nematodes of various species evidently feeding on the bacterial slime, several fungi preying on the nematodes,

[1] Thaxter, Roland. On certain new or peculiar North American Hyphomycetes. II. Bot. Gaz. **16**: 201–205. 1891.

amoebae of several types feeding on the bacteria as well as on the conidia of the nema-capturing fungi, and several species of minute phycomycetes preying on the smaller amoebae. The virtually complete degeneration of the *Pythium* mycelia had restored to the culture a degree of transparency little inferior to that of the medium originally; so that the delicate rangy hyphae of the fungus in question could be followed for long stretches with a water-immersion objective of high magnification. Optical conditions were therefore not unfavorable for uncovering possible mycelial relationships indicative of sarcophogy, opportunity for which the presence of fairly numerous dead nematodes and dead amoebae undergoing destruction by their fungous predators might be presumed to have supplied. However, even though occasionally somewhat denser branching could be made out in close proximity to a nematode freshly captured and killed, the visual evidence of sarcophagy was for the most part not especially striking. Yet the presumption for the fungus of a generally sarcophilous character comparable to that of Thaxter's species is perhaps not to be entirely dismissed, as some of the soluble substances in the dead microscopic animals could hardly have failed to diffuse into the agar substratum and thus become more widely available.

While in all phases of morphology and development the fungus under consideration shows close parallelism with *Helicocephalum sarcophilum,* its dimensions throughout are so much smaller as to leave no doubt that one is dealing with a distinct species. The vegetative hyphae are more delicate, measuring in diameter only slightly more than one-half of the 2.0 μ given by Thaxter. The fertile hypha which in Thaxter's fungus measures 1 mm. or more in height, here is usually only about one-half as tall. The basal diameter of the sporophore, which in the description of *H. sarcophilum* is given as 20 to 25 μ, is approximately only two-thirds as great in the present fungus, and an inferiority only slightly less pronounced is evident with respect to the apical diameter. In *H. sarcophilum* up to 21 spores are produced on one fertile hypha, whereas in the present form, rarely more than 10 are developed in a single head. Moreover the dimensions of the matured spores which in Thaxter's description are given as $55 \times 30\,\mu$ (maximum $65 \times 35\,\mu$) are represented in the present form by values nearly a

third less. As in spite of the smaller dimensions relative to *H. sarcophilum,* the new fungus is yet one of impressive proportions, a specific term having reference rather to the small number of spores is proposed as tolerably appropriate.

Helicocephalum oligosporum sp. nov.

Sparsum; hyphis sterilibus 1.0–1.3 μ crassis, fertilibus cylindraceis, sursum tenuatis, 0.35–0.6 mm. altis, 13–16 μ crassis, sursum 5.5–7.0 μ crassis; conidiis in spira 5–10, elliptico-cylindraceis, utrinque obtuse rotundatis, maturitate brunneis, 32–45 × 20–25 μ, demum secendibus et in capitulum subglobosum viscosum cohaerentibus.

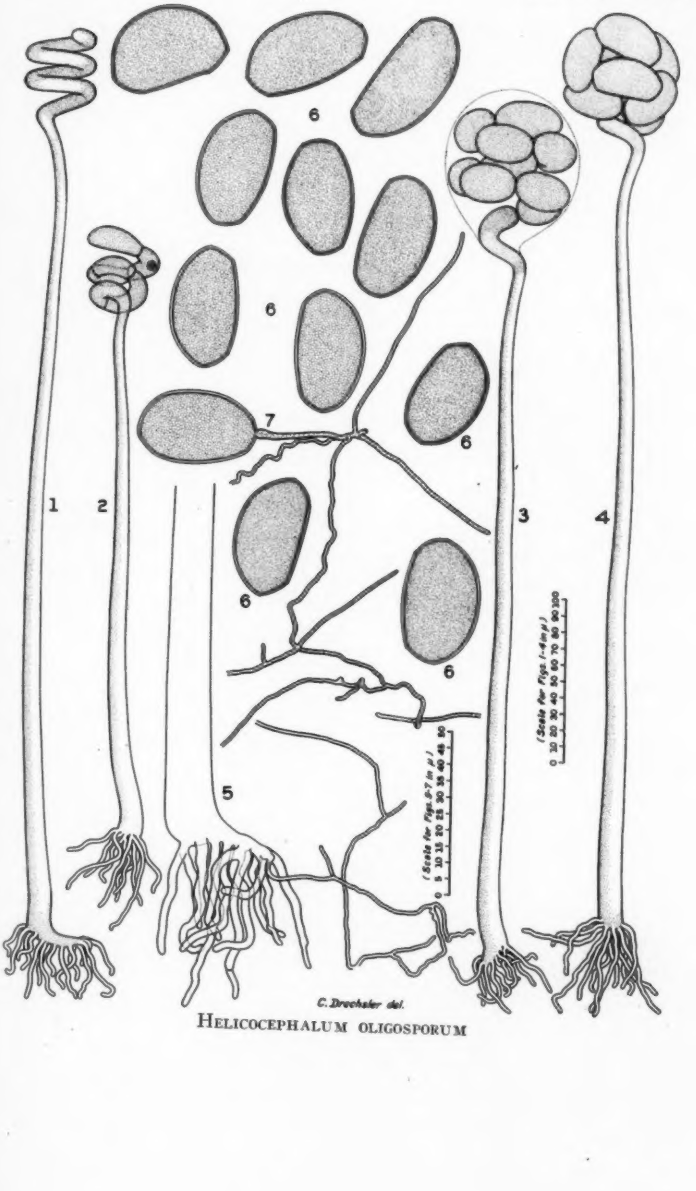
Sterile hyphae hyaline, creeping, rather sparsely branching, mostly 1.0 to 1.3 μ in diameter, devoid of septa except where living portions are contiguous to evacuated portions. Fertile hyphae sparsely scattered, hyaline, mostly 0.35 to 0.6 mm. in height, 13 to 16 μ in diameter at the base, where individually they are supported by rhizoids usually 10 to 20 in number and measuring 20 to 55 μ in length and 2 to 4 μ (average 2.7 μ) in diameter; tapering gradually upward to a diameter of 5.5 to 7.0 μ, then widening into a terminal portion abruptly coiled in usually 2 to 3 (mostly 2½) rather close helical dextrorse turns; the helicoid portion except for the proximal half turn, following insertion of septa at regular intervals, becoming converted at maturity into a chain of usually 5 to 10 spores. Spores brown, with finely granular contents, somewhat asymmetrically prolate ellipsoidal, obliquely truncate at either end (except terminal spore which is symmetrically rounded at distal end); provided with a wall mostly 0.5 to 1.0 μ in thickness; measuring 32 to 45 μ (average 38.7 μ) in length by 20 to 25 μ (average 22.5 μ) in diameter; separating and ultimately cohering in a rounded mass.

On laboratory culture prepared from decaying spinach (*Spinacia oleracea* Mill.) roots collected near Diamond Springs, Va., November 25, 1932.

Because of lack of evidence which might have referred *Helicocephalum sarcophilum* elsewhere, Thaxter prudently assigned the plant to the Hyphomycetes, adding, however, that it might eventually find a place among the Mucoraceae. In this connection the condition of the mycelium with respect to septation is deserving of some attention. The characterization of the sterile hyphae in the definition of the genus as " septate or rarely septate " would hardly encourage any very definite opinion concerning the taxo-

nomic affinities involved. Undoubtedly the difficulties attending the removal to microscopic mounts of vegetative mycelium from an opaque solid substratum in adequately extensive tracts must have been very considerable, and may have been only partly overcome. At any rate the rather meager representation of basal rhizoids in Plate XIX, Figure 1, accompanying the account suggests that a more than negligible degree of difficulty may have intervened even in the examination of these sturdier and more easily accessible structures. Such difficulty was fortunately not encountered in dealing with *H. oligosporum* in agar plate cultures, in which uninjured living vegetative filaments could be followed under high magnification to any lengths desired. The examinations thus facilitated revealed that whereas a septum was indeed present here and there, it always delimited a portion of filament filled with protoplasm from a contiguous portion of empty hyphal envelope. In no case were septa found inserted between adjacent masses of protoplasm within the vegetative thallus. In short the occurrence of septa was constantly associated with the evacuation or degeneration of protoplasmic contents in localized portions of originally continuous filaments, and was therefore thoroughly analogous to the occurrence of septa in the mycelium of the Phycomycetes generally.

The genus *Helicocephalum* may therefore with tolerable certainty be transferred to the Phycomycetes, apparently finding its most congenial place, as Thaxter well surmised, among the Mucoraceae. In this family, to be sure, it will occupy, hardly less than would have been the case in 1891, an isolated position; yet the isolation now becomes somewhat less conspicuous in view of the various other genera of curious morphology that have during the past four decades been definitely added here or are being assigned here with increasing confidence. As discovery of a sexual stage would be very useful in determining further the closer affinities of the genus, and since such a stage has not been found to occur hitherto in cultures of *H. oligosporum,* possibly because of a heterothallic condition, it is hoped that further strains of the same species may ultimately be found. Somewhat unfortunately the fungus has failed to grow in pure culture on any of the artificial media tried out so far, the spores failing to germinate and finally de-



C. Drechsler del.

HELICOCEPHALUM OLIGOSPORUM

generating when placed on sterilized agar substrata, though germinating fairly readily in the presence of contaminating bacteria and protozoa. For its conservation in living condition tube cultures representative of the same sort of biological mixture as that in which it originally made its appearance, have been successfully employed.

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EXPLANATION OF PLATE 4

Helicocephalum oligosporum. All figures drawn with the aid of the camera lucida, the magnification of those bearing numerals from 5 to 7 being exactly twice that of those numbered from 1 to 4. Fig. 1, Fertile hypha of approximately average definitive dimensions, showing basal rhizoids and terminal helicoid portion; × 250; 2, Fertile hypha of relatively small stature, after appearance of septa in the helicoid portion; × 250; 3, Fertile hypha after maturation of the brown spores, the original spiral arrangement of which is still maintained within the drop of extruded watery liquid; × 250; 4, Fertile hypha with ripe spores now disconnected but still cohering in a dry mass; × 250; 5, Basal portion of fertile hypha, showing connection with the mycelium from which it had origin, and relation to basal rhizoids; × 500; 6, Mature spores showing profile of each as viewed from along the axis of the spiral structure from which it originated; × 500; 7, Mature spore germinating with germ tube arising from truncate end; × 500.

ARTIFICIAL MANURE FOR MUSHROOM PRODUCTION [1]

SELMAN A. WAKSMAN AND C. A. RENEGER

(WITH TEXT FIGURE)

For the commercial production of mushrooms, horse manure, properly composted, was found to be, up until the present time, the only important substrate. All attempts to develop a compost from plant residues and inorganic fertilizer, without the aid of the digestive system of the horse, have so far given rather unsatisfactory commercial results, although the feasibleness of such a process has been definitely established (**1–4**).

Horse manure contains about 70 to 80 per cent moisture and about 2 per cent of nitrogen, on a dry basis; a part of this nitrogen is in a water soluble form, largely as urea and ammonia, and a part in an insoluble form, largely as protein. When horse manure is placed in composts and allowed to undergo aërobic decomposition, four distinct processes are found to take place (**5, 7**): (1) a gradual decomposition of the carbohydrates comprising the two major groups of these complexes present in the manure, namely, the cellulose and hemicelluloses; (2) a rapid transformation of the water soluble forms of nitrogen in the manure into insoluble organic nitrogenous compounds, accompanied by an increase in the relative total nitrogen content, because of the reduction of the total dry matter in the manure; (3) an increase in the relative content of the lignin and its derivatives, which resist rapid decomposition by the microörganisms active in the compost; (4) an increase in the relative ash content of the compost, parallel to the reduction of total dry matter, due to the accumulation of the mineral constituents in the process of decomposition; if no other data are available, one can measure the loss of total organic matter as a result of decomposition by the increase in ash concentration. When the total quantity of material in the compost has been re-

[1] Journal Series paper, New Jersey Agricultural Experiment Station, Department of Soil Microbiology.

duced to about 50 to 70 per cent of the original weight, as determined on a dry basis, the carbohydrates will be found to have been reduced to a considerably greater extent than the total material, the lignins to a less extent, while the mineral constituents will have increased in proportion to the disappearance of the organic substances; the protein content of the compost will have increased even more markedly, due to the synthesis of microbial cell substance by the microörganisms active in the decomposition of the various constituents of the manure (**5–8**). This is brought out in table 1.

TABLE 1

COMPARATIVE CHEMICAL COMPOSITION OF FRESH AND COMPOSTED HORSE MANURE [1]

Chemical Constituents	Per Cent of Total Dry Material		Per Cent of Ash-free Material	
	Fresh Manure	Composted Manure	Fresh Manure	Composted Manure
Fats and waxes	1.47	0.95	1.93	1.83
Cold water soluble organic matter	3.02	1.59	4.00	3.06
Hot water soluble organic matter	2.73	1.51	3.59	2.90
Hemicelluloses	11.28	5.79	14.84	11.13
Cellulose	25.05	12.59	32.96	24.21
Lignin	21.59	15.44	28.41	29.70
Total nitrogen	1.29	1.57	1.70	3.02
Water insoluble protein	5.94	8.56	7.82	16.46
Ash	24.1	47.8	—	—

[1] The fresh manure has been kept in a heap for several months and has already undergone decomposition, as compared with manure recently collected.

Horse manure, consisting of bedding (straw), droppings and urine, is a fairly well balanced medium for decomposition to proceed rapidly, so that it does not require any added material to result in a good compost; it must only be kept moist and aërated occasionally, when the temperature of the compost becomes too high. However, frequently even horse manure must receive some added material in order to result in a good compost: when the manure has been collected from stables which have been kept particularly clean, thereby not receiving a large part of the urine, the addition of a small amount of inorganic nitrogen salt will be

found to hasten the process of composting and will result in a much better compost; when the manure consists largely of droppings with too little bedding, the addition of some straw will be found to be very helpful in giving to the compost a better physical condition and in resulting in a better and more abundant substrate for the mushroom fungus.

With these elementary principles in mind, it is easy enough to proceed with the preparation from horse manure of composts for the growth of mushrooms. One has merely to follow well established practices. However, the problem becomes complicated when one attempts to produce composts only from plant residues. It becomes then essential to know the chemical composition of the plant material that is to be used, as well as to determine the nature and rate of its decomposition under different conditions.

In the preparation of composts from such plant residues as straw, which are poor in nitrogen and in the essential minerals, namely, phosphorus, potassium and calcium, inorganic salts have to be added to the compost, in order to enable the fungi, bacteria and other microörganisms which bring about the decomposition of the plant material to develop rapidly and hasten the process of composting. These microörganisms use the straw constituents, especially the carbohydrates, as sources of energy and the nitrogenous and mineral constituents for nutritive purposes, thereby transforming the latter into microbial cell substance. This can be most easily demonstrated by the transformation of the inorganic nitrogen compounds added to the compost into organic forms, namely, constituents of the microbial cells.

Lambert (**4**) found that in the preparation of artificial composts from straw, the temperature is never as high as in composts of horse manure, the latter usually reaching 65–72° C., while in the former 49° C. was the highest temperature attained. The reaction of the compost, as expressed by the pH value, is less uniform and the buffer content is lower in the artificial composts; this points to an insufficient decomposition, which may be responsible for the low yields of mushrooms obtained. Hein (**1, 2**) also reported poor yields from composts prepared from straw and inorganic fertilizer. An attempt was later made to use soy-bean stover and mixtures of stover and straw. Here, as well, the tem-

perature never reached higher than 49° C., except when horse manure was added. A period of 12 weeks was required for composting and the results obtained were no more encouraging than those with the straw alone.

In preparing composts from straw as the only plant residue, to which inorganic salts are added, several difficulties are encountered, chief among which is the slowness with which the straw becomes thoroughly wetted and the delayed attack of the straw by the microörganisms. Cereal straw in a mature state does not represent a very ideal physical and chemical medium for the activities of microörganisms. If one were to use, however, leguminous plants and other green materials high in water-soluble substances and in nitrogen, and low in cellulose and in lignin, for the preparation of composts, a soggy mass is obtained which represents a highly unfavorable medium for the growth of the mushroom mycelium.

As a result of numerous studies on the composting of various plant materials, alone and in combination, it was found that a certain balance between cereal straw and a plant material in a green state can form an ideal mixture for the preparation of a mushroom compost. The green material, whether freshly harvested or allowed to dry, will hold the water and absorb the added water readily and will begin to undergo immediate decomposition by microörganisms. The temperature rises rapidly and within a few days the compost is ready to be turned over. At that time a uniform composting mass is obtained. The green material will supply the microörganisms with some of the nitrogen and the minerals which are required for the decomposition of the straw, although additional inorganic salts will be required, the amount depending on the nature of the materials used and their relative concentration. This can be illustrated by presenting the results of a typical experiment carried out on a small scale in New Brunswick.

Four composts were prepared as follows: 1. horse manure, consisting of droppings and bedding, freshly collected from the local stable; 2. a mixture of wheat straw (60 per cent) and of tobacco stems (40 per cent); 3. 60 per cent straw and 40 per cent dry alfalfa hay; 4. 70 per cent straw and 30 per cent tobacco stems.

The composts of plant residues received also ammonium phosphate (16 per cent nitrogen), at the rate of 5 parts of the salt for 100 parts of the straw used in the composts. The composts were properly watered and allowed to decompose for 44 days, turning them at frequent intervals. The temperature changes in the four composts are shown in figure 1. Although before the first turning

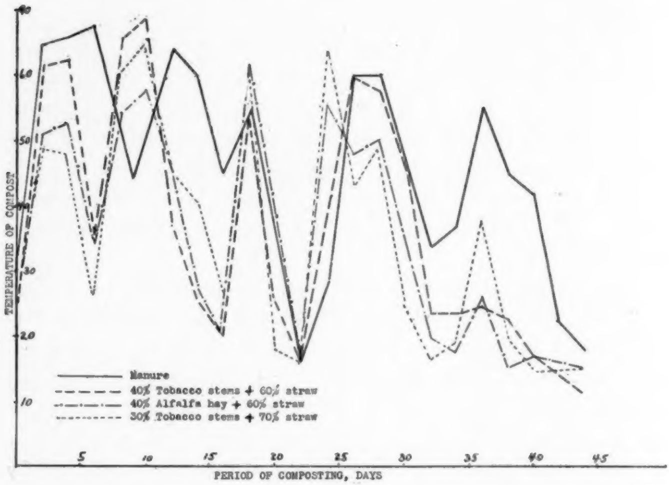

FIG. 1

the composts of the plant residues did not reach as high a temperature as that of the horse manure, after the first turning, the temperature of the former exceeded in all cases that of the latter.

The total dry weights of the composts at the beginning and at the end of composting are given in table 2, while the chemical composition of the dry material in the various composts is reported in table 3. The results show that the greatest loss of the organic matter took place in the compost consisting of straw and alfalfa, while the smallest loss occurred in the mixture containing 30 per cent tobacco stems and 70 per cent straw. As a result of the decomposition, there was a decrease in the water-soluble substances, in the fats and waxes and in the carbohydrates, accompanied by an increase in the mineral, protein and lignin constitu-

TABLE 2

DRY WEIGHT OF COMPOSTS AT BEGINNING AND END OF COMPOSTING

Number of Compost	1	2	3	4
Nature of Material	Manure	Straw (60%) + Tobacco Stems (40%)	Straw (60%) + Alfalfa Hay (40%)	Straw (70%) + Tobacco Stems (30%)
Total dry weight of material at start, lbs.	296.07	252.77	183.6	188.08
Total dry weight of compost, lbs.	182.20	138.04	67.34	124.21
Loss in weight, lbs.	113.87	114.73	116.26	63.87
Loss in weight, per cent	38.37	45.39	63.17	33.96

TABLE 3

CHEMICAL COMPOSITION OF COMPOSTS AT BEGINNING AND END OF COMPOSTING, PER CENT BASIS

Number of Compost	1 [2]		2		3		4	
	Start	End	Start	End	Start	End	Start	End
Moisture [1]	72.3	69.0	8.5	68.1	10.9	71.2	9.8	73.7
Total nitrogen in dry material	1.63	2.79	1.06	1.87	1.63	2.56	1.08	1.59
Total ash in dry material	15.74	24.97	19.72	32.14	8.68	13.35	15.81	18.75
Fats and waxes	2.24	0.74	1.57	0.92	1.88	1.17	1.55	1.52
Cold water soluble organic matter	4.93	2.63	9.96	3.49	8.77	4.47	8.13	3.27
Cold water soluble nitrogen	0.47	0.33	0.23	0.23	0.36	0.59	0.21	0.20
Total carbohydrates	39.35	24.83	40.26	30.85	51.73	45.00	44.90	42.41
Lignin	17.61	21.29	9.85	15.91	11.98	18.27	10.60	17.90
Crude protein	5.79	12.67	1.38	8.97	4.41	10.06	1.22	7.37

[1] In the case of the composts of plant residues, the moisture of the original material is given.

[2] See Table 2.

ents. The composts of the plant residues behaved as a whole in a manner similar to that of the horse manure, although some of the chemical constituents were transformed somewhat differently from a quantitative standpoint.

At the end of the decomposition period (44 days), the composts were transferred to regular mushroom beds, kept in a small, well ventilated dark room in the cellar of the building. The temperature of the room was then raised to 61° C. and the room thoroughly fumigated. A week later, the beds were spawned and

after the spawn was allowed to run for 28 days, the beds were cased with a light loam soil, to which 5 per cent of lime was added. The reaction of the composts was found to be about pH 8.0 in the case of the manure, somewhat more alkaline in the composts of straw and tobacco stems, especially where 40 per cent of the latter was used, and more acid in the case of the alfalfa-straw compost.

The spawn grew best on the alfalfa-straw composts, second best on the straw-tobacco stem composts and only third on the horse manure compost. The crop yields of the beds containing the various composts are given in table 4. The mushrooms began to

TABLE 4

YIELDS OF MUSHROOMS FROM COMPOSTS OF HORSE MANURE AND DIFFERENT PLANT RESIDUES

Average yield of bed, 8.16 square feet

Nature of Compost	Horse Manure	Straw (60%) + Alfalfa (40%)	Straw (70%) + Tobacco Stems (30%)	Straw (60%) + Tobacco Stems (40%)
Total yield, *grams* ..	3,798	2,550	3,989	416
Pounds per 1 square foot of bed space..	1.03	0.69	1.08	0.11

come first on the alfalfa-straw compost, next on the horse manure compost and only last on the straw-tobacco stems compost; the higher concentration of tobacco stems proved to be injurious to the production of the mushrooms, although not to the development of the mycelium. Whether this is due to the higher alkalinity of the composts or to the presence of a substance which in too high concentrations prevents the development of the mushrooms still remains to be determined.

The results show definitely that artificial composts can be prepared which are as satisfactory for the growth of mushrooms as horse manure. The greater degree of cleanliness, the better means of controlling the available material and the greater possibility for further improvement, all point to the probability of these composts taking in time the place of horse manure. However, the use of artificial composts will involve a greater knowledge of the chemical composition of the plant materials, of the processes of

decomposition of the plant residues in the compost and of the nutrition of the cultivated mushroom.

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THE SEXUAL MECHANISM OF SCLEROTINIA GLADIOLI [1]

F. L. Drayton

(WITH PLATES 5–7 AND 4 TEXT FIGURES)

Intensive cytological work has been done by several investigators on a few Ascomycetes, but in the majority of the genera there is no knowledge of the sexual mechanism involved in the formation of perithecia and apothecia. As a result, there is a dearth of fundamental information which would form the basis for any theories as to the phylogenetic relationships of this group and for a more thorough knowledge of the life histories of these fungi.

Cytological and experimental work with *Sclerotinia Gladioli* has revealed the presence of sex organs consisting of receptive bodies and microconidia; spermatization between compatible isolates being necessary for the production of apothecia. On the basis of this, in a paper to be published in Phytopathology, the writer proposes the new binomial *Sclerotinia Gladioli* (Massey) Drayton for the fungus previously known as *Sclerotium Gladioli* Massey, and includes a technical description of the fungus with illustrations of the sexual structures, and a brief historical resumé of the work on the fungus and the disease for which it is responsible.

It is only recently that the work on this organism has brought out these facts. In a preliminary account (**10**), the writer reported that the microconidia of *S. Gladioli* function as spermatia, and made reference to the structures in certain discomycetous lichens and in some of the Laboulbeniales, which are regarded as functional spermatia. Microconidia of the type found in *S. Gladioli* have been known for the past century and have been

[1] Contribution No. 124 from the Laboratories of Cryptogamic Botany, Harvard University.

Part of the work recorded here is taken from a thesis submitted to the Graduate School at Cornell University in partial fulfillment of the requirements for the degree of Doctor of Philosophy and the rest was done during the tenure of a National Research Fellowship in the Biological Sciences at the Laboratories of Cryptogamic Botany, Harvard University.

observed in species of the genera *Sclerotinia, Botrytis,* and *Sclerotium.* Their function has been a matter of much speculation, some authors considering them as functionless male cells, while de Bary (**2**), Brierley (**4**), and others have regarded them as true spores. We must pay tribute to the extraordinary insight of Tulasne who in 1863 described these structures (**15**), designating them as spermatia or conidiola, having prophesied in 1861 that, ". . . sometime or other it would be demonstrated that there resided in them a certain force or nature like that of pollen" (**14**). After Craigie (**7**) had demonstrated the sexual rôle of the pycniospores of the rusts, Whetzel (**16**) advanced the theory that these microconidia probably function as do the spermatia of the rusts. This has proved to be the case, for not only do the microconidia function as spermatia, but *S. Gladioli* and the rusts possess certain sexual phenomena in common. Later, Ames (**1**) working with *Pleurage anserina* (Ces.) Kuntze, has demonstrated the existence of sexual and genetical reactions in this fungus, which are similar in every respect to those found in *S. Gladioli.* As this situation was hitherto unknown in *Sclerotinia,* and involves indeed a new conception of sex in fungi, the results are presented here in detail.

EXPERIMENTAL DEVELOPMENT OF APOTHECIA

This fungus is known to develop mycelium, small resistant sclerotia, and microconidia. The sclerotia are minute structures, averaging $191 \times 164\ \mu$ in size, produced on the basal portion of the leaf sheaths and on the corm scales of diseased plants, and in and on all of the common culture media. Previous efforts to obtain sexually produced fruiting bodies were directed to the sclerotia, on the assumption that the fruiting bodies would be minute apothecia; but no such structures were produced in any of the trials.

Attention was then concentrated on a stromatic tissue as a possible source of fruiting bodies. Cultures on agar media develop a black tissue on their surface, but on sterilized wheat and water, this tissue is recognizable as a definite stroma, varying in thickness from 80–500 μ, and of different structure from the sclerotia. The latter have a compact rind and pseudoparenchymatous medulla,

while the stroma is prosenchymatous throughout, with a rind of loosely aggregated, black, septate, thick-walled, short hyphae (PLATE 7 E).

In the experiments with this stromatic tissue, portions of wheat cultures including the tissue were placed on moist sand and kept at 15° C. Some two weeks later, small, columnar, light brown, pilose structures, which were not apothecial fundaments, had developed from the stroma. With the hope that they might be receptive bodies awaiting fertilization by the microconidia, the following experiment was made. In four of these cultures, microconidial sporodochia from different isolates of the fungus were placed on the pilose structures with a needle. After 10 days, two lots showed definite development of elongated bodies easily recognizable as apothecial fundaments. The pilose structures had elongated and become branched, with less marked pilosity, darker color, and a depression at each tip; in this way resembling similar structures in the genus *Sclerotinia.*

When environmental conditions necessary for the development of apothecia had been determined, no difficulty was experienced in obtaining mature apothecia with asci and ascospores typical of those found in the genus *Sclerotinia.* The structure of this fruiting body is recorded in the separate paper to be published in Phytopathology. When the ascospores were discharged on potato-dextrose agar, they germinated in 8–10 hours and the resulting growth was identical with that of the original cultures.

Technique

The preliminary experiment provided some suggestion of the spermatial function of the microconidia and the receptive character of the pilose structures formed from the stroma. As indicated above, the confirmation of these results required considerable modification of the technique. This entailed primarily the determination of favorable cultural conditions for the development of microconidia and receptive bodies, and the procedures ultimately adopted for these phases of the work are described separately in the two succeeding sections of this paper. In addition, it was necessary to devise special methods for spermatization and for development of the apothecia, and these will be described here.

After several trials, a uniformly successful method for the process of spermatization was found. This involves a supply of suitable material, the preparation of a favorable soil extract, the application of a microconidial suspension to receptive bodies in the proper stage of development, and the maintenance of these at a suitable temperature. In addition, it was necessary to subject the fertilized cultures to appropriate conditions of light and temperature.

Material ideal for spermatization, was provided by wheat cultures in Petri dishes kept at room temperature for 17 days, followed by a temperature of 15° C. for 6–8 days. The contents of these Petri dishes were removed with a flamed scalpel and placed on a layer of sterilized, moist, sandy soil or sawdust, about ¾ inch deep in sterilized, 100 mm. preparation dishes. As a medium for making a suspension of the microconidia, a soil extract was prepared by intermittently shaking a mixture of 50 grams of soil and 500 cc. of distilled water for about an hour, filtering twice through filter paper, tubing, and then sterilizing for 30 minutes at 15 pounds pressure. By this procedure the soil extract was freed from any traces of copper in the distilled water, yielding a medium of an osmotic concentration comparable to that of the soil water with which the microconidia would be in contact in nature. A few drops of the soil extract were placed in a flamed watch glass, and into this, under the low power of a dissecting microscope, the microconidial sporodochia from the *Lycium*-potato-dextrose agar dishes were introduced with a flamed needle. The sporodochia were gently crushed with a flamed arrow-headed needle, so as to free the microconidia from their mucilaginous matrix. The suspension was then diluted with sufficient soil extract to obtain the amount required for spermatization; usually 8–10 drops of the suspension being sufficient for each Petri dish culture. Camel's hair brushes, sterilized by suspending them in boiling water for 15–20 minutes, were used for spreading the suspension over the receptive bodies, the brush being dipped repeatedly into the watch glass until the suspension was used up, if only one culture was to be spermatized. If, however, several cultures were to be spermatized, the suspension was dropped on the surface of each culture with a sterilized pipette and a separate

brush used to spread the drops over the receptive bodies. This precaution is necessary, because the wheat cultures often bear microconidia which would be introduced into the next culture spermatized. A layer of moist sandy soil or sawdust was then evenly distributed over the surface of the spermatized cultures, and a small quantity of plain soil extract added, so as to keep the upper and lower layers of soil or sawdust well moistened although not wet. The dishes were then placed in a 15° C. chamber.

Two kinds of test cultures were used in these experiments, in one of them, in addition to the spermatized plates, a second series of plates was subjected to similar treatment except that soil extract lacking microconidia was applied to the receptive bodies. In the other, to control the conditions still more exactly, and to make use of comparable portions of the same thallus, the cultures before being removed from the Petri dishes were cut in half, and the two halves spaced an inch or so apart on soil in a Stender dish. One half was then spermatized and the other half treated similarly with plain soil extract (PLATE 6*A*).

Further treatment of the cultures in which fertilization had been accomplished was as follows. After the apothecial fundaments became evident, usually in 8–10 days, they were kept under observation for another 4–6 days, when the depression at their apices was well defined. At this critical stage, they were removed to the light at a temperature maintained as near 15° C. as possible, direct sunlight being avoided by using a cheesecloth covering about 2 feet above the cultures. During the winter and early spring the greenhouse was satisfactory for this purpose, the apothecia expanded and matured in 12–18 days, depending on the amount of light prevailing, but as the season progressed it became necessary to use artificial light in a controlled cold chamber. Here the light was supplied by 60 watt, frosted, electric bulbs in gooseneck lamps, so placed that the bulbs were two feet above the covers of the dishes.

Experimental proof

Using the technique described above, extensive experiments were conducted with ten isolations of the fungus, which had been collected during the preceding years from various localities and

suscepts. The original designations of these cultures are here listed with brief descriptions.

G5—From a corm of one of the large flowering gladiolus varieties in a shipment from Holland, 1926.

SG2, SG3, SG4—From corms of large flowering and primulinus hybrid varieties of gladiolus grown in New York State, 1929–1931.

Gnl—From a corm of one of the small flowering or Colvillei type of gladiolus in a shipment from Holland, 1926.

C2—From a crocus corm collected in Holland in 1928.

Fla—From a freesia corm in a shipment from Southern Europe, 1927.

Flb, F2—From freesia plants collected in Long Island, N. Y., in 1929 and 1932 respectively.

S360—From gladiolus corms collected in Indiana in 1926.

Monomycelial transfers were made from these cultures by means of single hyphal tip isolations, and their specific identity was established by the uniformity of their growth and size of sclerotia on various culture media, and by successful inoculation in and on young gladiolus corms.

Each of the ten cultures is capable of producing both receptive bodies and microconidial sporodochia, which makes it possible to carry out reciprocal crosses between all of the isolates. In conjunction with adequate test cultures, this was done, and in the accompanying diagram, those crosses which resulted in apothecia are indicated by the symbol +, and those in which no fertilization occurred, by the symbol —.

Figure 1. It is evident that the receptive bodies of each isolate cannot be fertilized by microconidia from the same thallus, that is, they are self-sterile. In addition, three of the isolates are compatible with the other seven. Two groups are therefore represented in these ten isolates, one comprising C2, F2, and S360, and the other G5, SG2, SG3, SG4, Gnl, Fla, and Flb. These groups exhibit reciprocal inter-group fertility, reciprocal intra-group sterility, and self-sterility in every isolate.

Single and multiple ascospore cultures were made from discharged ascospores, 24 of the former and 5 of the latter, using apothecia from two different crosses. These cultures were planted

in duplicate on sterilized wheat in Petri dishes and when the receptive bodies appeared, one series was spermatized with microconidia from the isolate used as a source of receptive bodies in the original cross, and the other series was spermatized with microconidia from the isolate used as a source of microconidia in the

♂ \ ♀	G5	SG2	SG3	SG4	GN1	F1a	F1b	C2	F2	S360
G5	—	—	—	—	—	—	—	+	+	+
SG2	—	—	—	—	—	—	—	+	+	+
SG3	—	—	—	—	—	—	—	+	+	+
SG4	—	—	—	—	—	—	—	+	+	+
GN1	—	—	—	—	—	—	—	+	+	+
F1a	—	—	—	—	—	—	—	+	+	+
F1b	—	—	—	—	—	—	—	+	+	+
C2	+	+	+	+	+	+	+	—	—	—
F2	+	+	+	+	+	+	+	—	—	—
S360	+	+	+	+	+	+	+	—	—	—

Fig. 1. The result of reciprocal crosses between ten isolates of *S. Gladioli*. The symbol + indicates development of apothecia, the symbol — the absence of fertilization.

original cross. In other words, the receptive bodies developed from hybrid ascospores were back-crossed separately with each of the parent isolates. The results were highly significant, for the multiple ascospore cultures reacted with the microconidia of both parents, 12 of the single ascospore cultures reacted with the isolate used as a source of microconidia—the male parent, and the other

12 reacted with the female parent isolate. The number of cultures used is obviously too small to draw any definite conclusions as to the segregation ratio of the compatibility or sterility factor, but it is evident that segregation does take place and apparently in a 1 : 1 ratio.

In this and many other species of *Sclerotinia,* it has been observed that the ascospores, when placed in a comparatively non-nutritive medium such as soil extract or tap water, develop microconidia directly on the spores or on short germ tubes. These microconidia are capable of fertilizing receptive bodies, as shown by the following two experiments. The isolate C2 was planted on the cut surface of cooked gladiolus corms and in due time receptive bodies were produced in abundance. Two groups of these were spermatized with microconidia of the compatible isolate Gnl and in 10 days apothecial fundaments were well developed in the spermatized areas (PLATE 5 A), and these expanded into mature apothecia in two weeks and ascospores were discharged. Three weeks later, it was noticed that the surrounding receptive bodies, which had not been spermatized, were beginning to develop into apothecia (PLATE 5 B), which later matured, the original two groups of apothecia having dried up in the meantime. Under the moist conditions prevailing in these cultures, the ascospores which fell on the receptive bodies had presumably developed microconidia and some of these, approximately half of them, were capable of fertilizing the receptive bodies which had not been included in the two areas originally spermatized. To substantiate this assumption, six cultures bearing receptive bodies and consisting of isolates representative of both groups, were placed on moist sandy soil in preparation dishes, and four mature apothecia were attached to the lid of each dish so that the ascospores could be shot downwards to the receptive bodies. The apothecia used for this experiment were all the product of cross-spermatization between the isolates C2 and Gnl. In 10 days the six cultures were covered with apothecial fundaments, thus indicating that fertilization had been accomplished by the microconidia formed by the germinating ascospores. The segregation of the compatibility factor in the ascus therefore resulted in a condition whereby the microconidia produced by approximately half of the ascospores discharged by any

one apothecium were apparently compatible with the receptive bodies of any one isolate.

In order to prove that the development of apothecia was brought about by the fertilizing power of the microconidia rather than as the result of the stimulating action of some substance secreted by them, the following experiment was performed. A soil extract suspension of microconidia was made and half of it was filtered through a Berkefeld filter, which removed all of the microconidia. The filtered and unfiltered portions were then applied separately to four dishes with cultures bearing receptive bodies of two compatible isolates. Each portion was used on two cultures, one of one isolate and the second of the other. Optimum conditions of temperature and moisture were provided, and at the end of 14 days it was evident that the two dishes spermatized with the unfiltered suspension had developed apothecial fundaments, while a microscopic examination of the two cultures to which the filtered extract had been added, failed to show any development of the receptive bodies indicative of fertilization.

All possible vegetative pairings of the ten isolates were made to determine whether fertilization could be effected by the intermingling and fusion of hyphae of the thalli of any pair of isolates. These were kept under optimum conditions, but no apothecial fundaments appeared. On later flooding the preparations with water, and so washing a few microconidia from one thallus to the other in each plate, a few apothecia were produced where compatible pairs were present. None appeared where incompatible isolates were paired. It is obvious therefore that fertilization cannot be brought about as a result of hyphal fusion.

The microconidia of this fungus are therefore true spermatia or gametes, capable of fertilizing receptive structures formed on the stromata of certain other thalli with the consequent development of apothecia. The phenomenon of self-sterility and fertility only between certain isolates is significant, but not new among plants, for observations of this character have been made in several genera of hermaphroditic flowering plants.

The microconidia

Massey (**13**) first observed microconidial sporodochia in test tube cultures 25–40 days old, where they appeared as minute white granules buried in the medium and adjacent to the wall of the tubes. The writer made an effort to provide cultural conditions which would be more favorable for their production. Media composed of the stems of various plants combined with potato-dextrose agar were tried, and it was found that the stems of matrimony vine (*Lycium halimifolium*) used in this way in Petri dishes and kept at room temperature for 2–3 weeks provided the desired conditions. It is of interest to note that when sterilized soil is placed in a channel made by removing a strip of agar from the center of a Petri dish of solidified potato-dextrose agar, and the fungus planted on either side of the soil, microconidia develop in abundance on hyphae that penetrate the soil. Again, when sterilized soil is placed on two weeks old cultures of any favorable medium, sporodochia will develop in the soil. This is not a practicable means of obtaining microconidia for purposes of spermatization, but it indicates that these spores are probably formed in nature in the soil surrounding diseased plants.

Figure 2. The sporodochia appear at first as small milky droplets which later enlarge up to 1.5 mm. in diameter, become more opaque, and on drying become waxy in consistency. They consist of a central core of intertwined conidiophores arising from closely septate hyphae, which develop as branches from a main hypha running through the center of each sporodochium. Each conidiophore is verticillately branched and the ultimate branches are elongate, tapering cells which are curved and cut off microconidia exogenously from their apices in the form of loosely connected chains. A short isthmus is often evident connecting the spores with the terminal cells and this often remains attached to some of the spores. The microconidia are cut off in immense numbers and are embedded in a mucilaginous matrix which becomes waxy on drying, but is easily soluble in water. The microconidia are globose, 1.2 to 1.8 μ in diameter, hyaline, and contain a single nucleus which occupies about one third of the volume of the spore. When viewed in various positions of the spores the nucleus is seen to be cup-shaped (FIGURE 2).

Most investigators, including the writer, have failed to obtain any growth of the microconidia of this or other species of *Sclerotinia*. The few cases where successful germination is reported, remain to be satisfactorily explained.

Fig. 2. A small microconidial sporodochium showing the conidiophores and the microconidia embedded in a mucilaginous matrix. Inset—some microconidia more highly magnified showing the shape and size of the nuclei.

The cultural conditions best suited to the production of receptive bodies are usually not favorable for the development of microconidia and vice versa. In a few of the matrimony vine and potato-dextrose agar plates, however, small stromatic areas were formed on portions of the stems close to the surface of the agar and these patches of stroma developed a few receptive bodies,

on which microconidial sporodochia later appeared (PLATE 6 B). This provides spectacular evidence of the monoecious or hermaphroditic character of a monomycelial thallus of this fungus, and, as these receptive bodies did not develop apothecia, the self-sterility of each isolate was again demonstrated.

THE STROMA AND RECEPTIVE BODIES

The stroma forms a discontinuous, partly separable layer on the surface of solid substrates rich in starch such as grains of wheat, rye, barley, etc., but on nutrient media like oatmeal, cornmeal, potato-dextrose agar, etc., the layer is a continuous and inseparable one. This difference is due to the uniform ease with which the hyphae can penetrate the latter media, while on grains of wheat only certain portions appear to be easily penetrable, notably the vicinity of the embryo. At these points the hyphae become established within the grains early in the development of the fungus, and later as the stroma develops it spreads over the rest of the grains in a separable and much thinner layer. The development of the receptive bodies takes place from these thicker stromatic areas, the amount of stored material there being obviously greater. In nature the stroma is only found in the corms of diseased plants, thus accounting for the necessity of a culture medium rich in starch for its development in the laboratory.

The structure of the stroma and its difference from that of the sclerotia has already been noted. The sclerotia apparently function solely as organs of resistance, while the stroma is the specialized tissue for the production of receptive bodies and apothecia. This is different from the situation in the species of *Sclerotinia* with true sclerotia so far studied, in which these two functions are combined in the one structure. This striking difference will be referred to again in a later section of this paper.

The receptive bodies are .8–1.9 mm. tall depending on their age, .4–.8 mm. broad, columnar, sometimes branched or cockscomb-shaped, tapering to a rounded apex or occasionally slightly capitate, light brown, pilose, and surrounded with a thin layer of mucilaginous substance. Externally, they possess a layer of loosely interwoven, thick-walled, septate hyphae, which are hyaline towards the apex, but become progressively darker towards the

base, merging with the black hyphae of the stromatic rind which may extend upwards to a distance of about one third the length of the receptive body. Within this are light brown, densely packed and intertwining longitudinal hyphae which at the apex give rise to a crown of thinner walled, septate, densely filled hyphae, which arch inwards to form a depression at the center of the apex (PLATE 7 A AND B.). In the center is a column of hyaline, less compact tissue tapering more or less sharply to the apex and consisting mainly of a sparsely septate, intricately coiled, multinucleate ascogonial system which terminates at the apex in trichogynous hyphae with their tips clustered beneath the overarching, sterile hyphae at the apex of the receptive body (PLATE 7 C AND D).

In order to determine the optimum conditions for the development of receptive bodies, the following experiment was carried on. The isolates G5, SG4, Gn1, C2, F1a, and F2 were grown at temperatures ranging from 12° to 30° C. at intervals of 3° and also at room temperature (18°–21° C.). The cultures used consisted of wheat grains and water in the proportions of 1 to 3 by weight, placed in Petri dishes, and sterilized at 15 lbs. steam pressure for 30 minutes. The plates were planted in a duplicate series and held at the various temperatures for 17 days, after which they were placed at 15° C. for 10 days, when notes were taken on the prevalence of the receptive bodies. The accompanying charts illustrate the results obtained.

Figure 3. It is evident that all of the isolates have their optima for receptive body formation within the range 18° to 24° C. Certain individual variations are exhibited, however; C2 and F1a are at the extremes as regards the readiness with which receptive bodies are produced. This variation is correlated with individual differences in rate of growth as determined by daily measurements of the thalli during the first 72 hours of their growth. Where no receptive bodies developed at 12° C. and at 30° C., there was no stroma present, and an increasing number of receptive bodies at the other temperatures was accompanied by increased amount of stroma.

Under these optimum conditions, the development of the receptive bodies is initiated by a protrusion on the surface of the stroma, which quickly elongates, leaving the black stromatic rind

towards the base of the receptive body. Prior to this, when the surface of the stroma is still flat, beneath the rind a clump of deeply staining, coiled hyphae may be seen, which have no connection with the surface. These hyphae apparently constitute the initials of the coiled ascogonial system (PLATE 7 E).

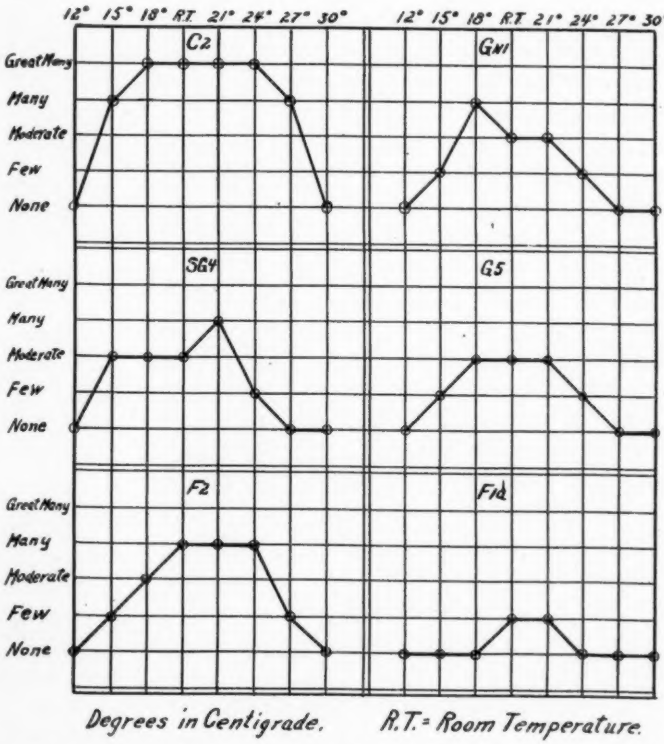

Fig. 3. Charts showing the relation of temperature during vegetative growth of the mycelium to receptive body production, in six isolates of *S. Gladioli*.

It was of importance to determine whether fertilization was restricted to the receptive bodies and the following experiment was devised with this end in view. A single receptive body was spermatized with a small amount of microconidial material from

a compatible isolate, and precautions were taken to prevent the spread of microconidia to neighboring receptive bodies. Some branching of this receptive body took place after spermatization, and each branch developed into an apothecial fundament. The surrounding receptive bodies had also branched and elongated slightly, but showed no evidences of fertilization. In this experiment, microconidia were also placed on stromatic areas from which receptive bodies had not yet developed, and there was no reaction of any kind. This proves that the receptive bodies alone possess the facilities for fertilization, the ascogonial coil being inaccessible prior to the development of the receptive bodies.

In another experiment with the same object in view, a series of 15 wheat cultures was planted with the isolate C2. Leaving plates 1, 7, and 15 unspermatized, the others were spermatized with microconidia from the compatible isolate Gn1, commencing with plate 2 on the fourth day after planting, and continuing at intervals varying from 1 to 3 days to plate 14, where spermatization was performed on the 23d day, when a considerable number of receptive bodies had appeared. All of the cultures except No. 14 and the checks were spermatized before any receptive bodies had formed. The whole series was then covered with moist sandy soil on the 23d day and put at 15° C. After two weeks, the first nine cultures in the series, spermatized between the 4th and 16th days showed a few apothecia developing in some, none in others. The 10th and 11th cultures, spermatized on the 18th and 19th days, just before the receptive bodies became plainly evident, had quite a large number of young apothecia. The 12th culture, however, spermatized on the 23d day when a great many receptive bodies were present, had an immense number of apothecial fundaments and the unspermatized ones had none. The fact that a few apothecia developed in certain cultures spermatized before receptive bodies appeared, indicates that some microconidia remained viable until receptive bodies developed. Fertilization could not have occurred through the stroma, for this possibility was eliminated by the experiment described above, and this experiment further excludes any possible interaction between microconidia and vegetative hyphae.

The development from receptive bodies to apothecial fundaments, or the failure of this to occur, is evident 10 days after spermatization. In the test cultures, in the self-spermatized cultures and in those spermatized with microconidia from an incompatible isolate, fertilization does not occur, as has been previously shown. This can be recognized macroscopically by the slight elongation of the receptive bodies, without change of appearance, and by the development of white patches of mycelium on the soil surrounding the receptive bodies; presumably a vegetative proliferation. The cultures in which crosses were made between compatible isolates soon show evidences of fertilization, by the absence of any mycelial patches and the apothecial fundaments are evident as short, black, erect columnar bodies, glistening with water, and with a slight depression at the apex (PLATE 5 A).

PRELIMINARY CYTOLOGICAL OBSERVATIONS

In view of the interesting results obtained in the experimental work on the sexual mechanism of *S. Gladioli*, some cytological studies were undertaken. No investigation of this kind has ever been made of any species of *Sclerotinia*, except that of Kharbush (**12**) who attempted to trace the nuclear evolution in the ascus of *Sclerotinia Fuckeliana* de Bary. In longitudinal sections of the apothecium he found binucleate cells in the ascigerous layer arising from two mycelial filaments which anastomosed at their apices and were separated from these branches by a septum. He traced the development of the asci from these cells and considered that the association of nuclei is accomplished at the point of anastomosis in a manner similar to that described by Dangeard (**8**) for *Peziza vesiculosa*. This author regards the situation in *Peziza* as analogous to that of *Eremascus* and *Dipodascus*, although he qualifies this statement by an observation that frequently the young ascus appears to have a different origin in which a "crozier" is involved. It is obvious that Kharbush's conception of the origin of the ascus is a misinterpretation, as he failed to recognize the sexual function of the microconidia, but his contribution lies in his description of the nuclear phenomena involved in the developing ascus, where he observed nuclear fusion to take place, and also described the subsequent divisions leading up to

the formation of the 8 ascospores. He is emphatic in his observations that the chromosome numbers of the fusion nucleus and nuclei after reduction division are four and two respectively.

In an attempt to trace the nuclear history of *S. Gladioli*, receptive bodies, apothecial fundaments, and apothecia were killed, imbedded in paraffin, and eventually stained in iron-alum haematoxylin and erythrosin. One series was spermatized with compatible microconidia, and then at daily intervals a number of receptive bodies were removed and killed; thus giving stages which were representative of the entire development of the fruiting body. Another series paralleled the first, but in this instance incompatible microconidia were used for spermatization. In both of the series some receptive bodies also were killed and fixed before the application of microconidia.

Many difficulties were encountered in devising a satisfactory technique for this study, and the complex structure of the receptive bodies tended to obscure many details of the nuclear history. In spite of these difficulties it seems desirable to record various points of interest that have come out of this preliminary cytological study.

Figure 4. The vegetative mycelium comprises cells containing usually 4 nuclei of approximately .5 μ in diameter. The microconidia borne on this mycelium have a single, cup-shaped nucleus that occupies about one third of the volume of the spores (FIGURE 2). The sparsely septate, coiled ascogonial hyphae show great variability in size, shape, number, and distribution in different receptive bodies. Similarly their many nuclei differ in size and number in the various cells of these hyphae (FIGURE 4 A). Considerable anastomosis takes place between the cells of the individual coils. The coils in turn give rise to elongate, almost straight hyphae which by the fact that they are less densely stained and of greater diameter, may be distinguished from the sterile apical hyphae that arch above them. These straight elongate hyphae are trichogynes because they disintegrate after spermatization with compatible microconidia, while at the same time the ascogonial coil exhibits decided modification, as will be described.

The microconidia, when placed on the receptive bodies are either drawn by capillary action into the channel formed by the apical hyphae and so brought into contact with the trichogynes.

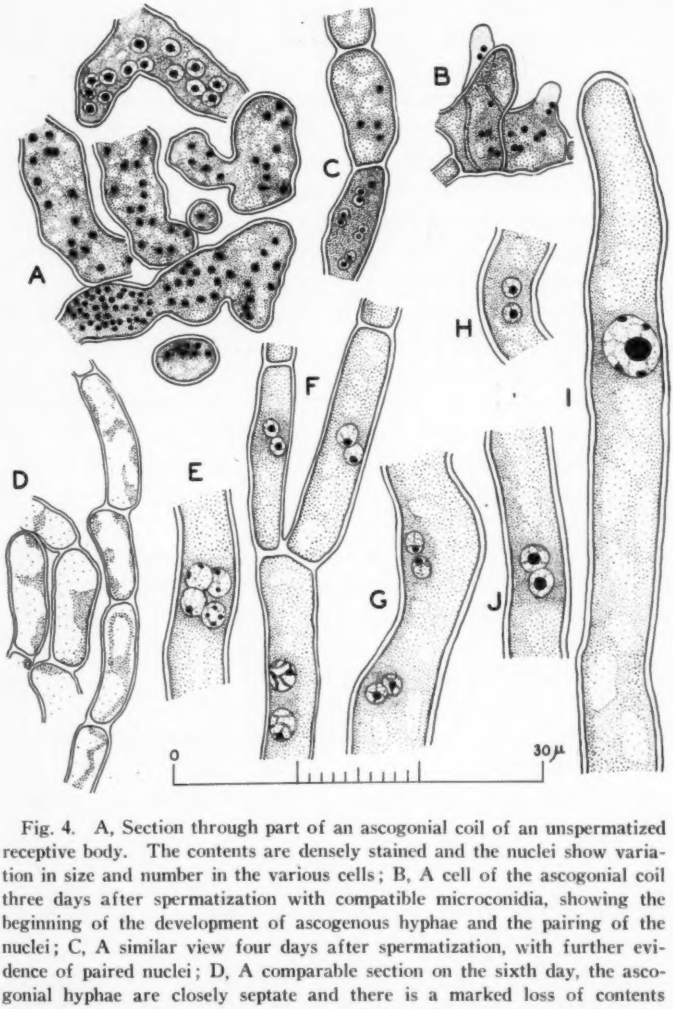

Fig. 4. A, Section through part of an ascogonial coil of an unspermatized receptive body. The contents are densely stained and the nuclei show variation in size and number in the various cells; B, A cell of the ascogonial coil three days after spermatization with compatible microconidia, showing the beginning of the development of ascogenous hyphae and the pairing of the nuclei; C, A similar view four days after spermatization, with further evidence of paired nuclei; D, A comparable section on the sixth day, the ascogonial hyphae are closely septate and there is a marked loss of contents and reduction in the width of the cells; E, F, and G, On the 24th day with the apothecium nearing maturity. Various stages of conjugate division in the ascogenous hyphae. Note the branching in F; H, I, and J, Parts of young asci on the 26th day; H, the nuclei just prior to fusion; I, The fusion nucleus; J, the daughter nuclei from the first division of a fusion nucleus.

or they are held in the depression, submerged by the growth of the surrounding apical hyphae, and met by the elongating trichogynes. The migration of the nucleus from the microconidia and its subsequent passage to the ascogonial coil was not observed.

Receptive bodies spermatized with incompatible microconidia, elongate but slightly, and the structure of the coiled ascogonial hyphae does not exhibit any change even after 15 days. Where compatible microconidia have been used, however, decided modification of the coil is evident at the end of 3 days. The condition of sparse septation is changed to one of frequent septation and each of the resulting cells becomes markedly swollen. During the 4th day the nuclei become definitely paired and the coil gives rise to short protuberances (FIGURE 4 B). The 5th day marks the commencement of the degeneration of the terminal hyphae of the coil, and at the same time the protuberances on the coil can be identified as the branches which are destined to be the ascogenous hyphae. From then onward, rapid development of the ascogenous hyphae occurs, conjugate division of their paired nuclei is evident (FIGURE 4 E, F AND G), and the coiled ascogonial hyphae, on the 7th day, lose their identity through loss of their contents (FIGURE 4 D). Following this, rapid elongation of the apothecial fundament occurs, the apical hyphae gradually take the form of paraphyses, beneath which the ascogenous hyphae are developing. By the 26th day, the apex has begun to expand, the paraphyses are organized into a hymenium and the apices of the much branched ascogenous hyphae are in the subhymenial area. Between the 26th and the 30th day the young asci can be identified as they push their way through the paraphyses. At this stage were observed in the developing ascus the two nuclei prior to fusion (FIGURE 4 H), the fusion nucleus (FIGURE 4 I), and the daughter nuclei resulting from the first division (FIGURE 4 J). The stages between the first division and the early stages in the formation of the ascospores were not evident in the present preparations, but spores that have just been delimited are uninucleate, a condition which persists until just before germination, when this nucleus divides.

No definite statement can be made as to chromosome number. All of the material was killed during the day and the scarcity of

meiotic or mitotic figures in all of the preparations, indicates that the nuclear divisions probably take place at night. These investigations are being continued in the hope that the points now in doubt will be cleared up and that the gaps in the cytological story of this sexual mechanism will be filled in.

THE PROBABLE OPERATION OF THIS SEXUAL MECHANISM IN NATURE

The apothecia, receptive bodies, and microconidia of *S. Gladioli* are developed readily in artificial cultures, but none of these structures has been observed in nature. As stated previously, there is good evidence to believe that the microconidia are formed in the soil in the vicinity of diseased plants, and the presence of the stroma in badly diseased corms indicates that the receptive bodies and apothecia are probably developed from these organs. Favorable conditions of moisture and temperature and the close proximity of compatible thalli would of course be prerequisite factors for the development of apothecia.

The phenomena of self-sterility, and fertility only between compatible forms, leads us to a consideration of possible spermatizing agencies in nature. The mucilaginous material in which the microconidia are embedded would protect them from dessication during periods of drought. This substance is soluble in water, and on account of the minuteness of the spores, they may well be transported through the soil in moving water. Their sticky nature may also allow the sporodochia to adhere to the bodies of soil-inhabiting animals or insects, and so be carried through the soil, possibly to receptive bodies of a compatible thallus.

This fungus is apparently well adapted to prolonged existence in the vegetative stage. The sclerotia will withstand freezing and drought. This, with a possible saprophytic existence in periods favorable for development, enables the fungus to remain alive in soil for many years, even when no susceptible plants are present in the interval. It remains alive in corm lesions during storage, so that the sale and transportation of diseased stock assures dissemination within and between countries and continents.

The fact was previously noted, that in this fungus the resistant structures and the specialized tissue for production of sexually

formed fruiting bodies are separate entities. This is in contrast to the species of *Sclerotinia* having true sclerotia, in which the latter function in both ways. The fact that in other species of *Sclerotinia* the development of receptive structures has never been noted is significant. Apparently in these forms spermatization and fertilization occur before any external development of the sclerotium is evident, and apothecial fundaments then develop when environmental conditions are favorable. The different sequence of events in the case of *S. Gladioli* may be accounted for by the facts that the whole process takes place below ground and that the thalli are self-sterile. With the microconidia borne in the soil, the development of prominent receptive bodies from the diseased corms would greatly enhance the chances of cross-spermatization, especially if soil animals or insects are the principal agency for this purpose. It is possible also that the musty odor emitted by this fungus may have a special attraction for such an agency. This mechanism differs materially from several other species of *Sclerotinia* which must exhibit self-fertility, for cases are on record (**9**, **11**) where apothecia have been obtained from sclerotia developed in monoascosporic cultures. In these cases, the microconidia are borne in contact with the sclerotia, no spermatizing agency is required, and the presence of trichogynous hyphae on the surface of the sclerotia, without any receptive body, would provide an adequate mechanism for fertilization.

The occurrence of this fungus on its various suscepts in their natural habitats has not been recorded. The genera included, comprise plants of both tropical and temperate origin, so that one cannot draw any conclusions as to the climatic zone or suscept in which the fungus may have had its origin. The *Sclerotinia* spp. so far described have been mainly from the temperate zones, but as far as this fungus is concerned, on the gladiolus it seems likely that, in temperate regions at least, the conditions under which it is grown are not favorable for apothecial development. In these regions the corms are harvested in the fall, kept in storage during the winter months and replanted in the early summer, and even if compatible thalli should be present in close proximity and a suitable spermatizing agency present, the temperature conditions while the plants are in the ground would not favor the development

of the sexual stage. In somewhat warmer regions, where it is possible to leave the corms in the field during the winter, the chances of getting apothecia would be greater. The crocus lives the year round in the soil in temperate regions, and it is possible that the sexual stage may develop on this plant, and perhaps the fungus was introduced with it.

It is as yet unprofitable to speculate on the distribution of the two interactive groups of the fungus in nature. In the ten isolates used in this work, the two groups are not segregated on geographic distribution or according to suscepts. In one group there are crocus, freesia, and gladiolus isolates from Holland, Long Island, N. Y., and Indiana respectively. In the other group are two types of gladiolus, and freesia isolates from Holland, Southern Europe, and New York. In any case, no significance could be attached to the source of the diseased material, because of the world-wide movement of corms of all of the suscepts.

DISCUSSION

In the large assemblage comprising the group of sclerotium-producing fungi of ascomycetous affinities, the proportion of the species in which the perfect stage has been found is surprisingly small. This is true, notwithstanding the fact that microconidia, of the type here described, have been observed in many of them, but only a few forms commonly referred to the form-genera *Botrytis* and *Sclerotium* have been connected with species of *Sclerotinia*. From the results obtained in this investigation, it seems probable that many species of these form-genera may in reality possess perfect stages which are as yet unknown because these fungi are self-sterile. It is reasonable to suppose that morphologically identical microconidia occurring in other species may function sexually as do the microconidia of *S. Gladioli.* Yet on the other hand Godfrey (**11**) and Dickson (**9**) report that it is possible to obtain apothecia from monoascosporic cultures of *Sclerotinia Ricini* and *S. sclerotiorum* respectively. In these species, a homothallic condition must exist, but differing from *S. Gladioli* in that they must be self-fertile and the spermatia must be borne in contact with the receptive hyphae, for no spermatizing agency could be operative in undisturbed cultures.

As one attempts to apply experimentally the sexual principles found in *S. Gladioli* to other species, differences in the sexual apparatus will almost certainly be found. For example, clearly differentiated receptive bodies may be exceptional; the trichogynes may be borne singly or in small groups on the surface of sclerotia or stromata, unassociated with any distinctive structure. It is hoped that this investigation will stimulate work along this line and that the apothecial stage of many imperfect forms may be discovered. Such work would undoubtedly assist in clarifying the taxonomic and phylogenetic relationships in this group.

The question of hybridization between distinct species or between physiological forms also enters into this discussion. The sexual function of the pycniospores in the rusts has led to the demonstration of the creation of new pathogenetic races by appropriate combinations of pycnia and sporidial thalli. There is an indication of the presence of pathogenetic races in certain species of *Sclerotinia* and *Botrytis* and it is highly probable that these have been brought about by cross-fertilization.

No reference has been made throughout this paper to the question of heterothallism as applied to the results obtained with *S. Gladioli.* It is felt that the phenomenon to which this term was originally applied is different from the one in *S. Gladioli,* and that the application of the same term here would be incorrect. It was Blakeslee (**3**) in 1904 who first used this term and defined it when, in discussing the results obtained with *Rhizopus,* he stated, " The condition is similar to that in dioecious plants and animals. . . . Inasmuch, however, as conjugation is possible only through the interaction of two differing thalli, we can express this fact by calling all species the sexual relations of which correspond to the *Rhizopus* type *heterothallic.* In marked contrast to the conditions just described, *Sporodinia* and the other members of the group of which it is the type, invariably reproduce sexually under suitable conditions when grown from a single spore. The zygospores thus originate from a single mycelium, and are comparable to hermaphrodites among the higher plants. Such forms may, therefore, be called *homothallic.*" It seems quite clear from this and later papers that he applied the term heterothallism to a condition in which segregation of sex occurs in such a manner that some

thalli are wholly male, while others are wholly female. It seems reasonable to assume that he would also include in his concept of homothallism, monoecious species in which the thallus is self-sterile.

It is true that the condition existing in *S. Gladioli* is heterothallism in the literal sense of the word. Two groups of thalli exist which differ in a physiological factor which determines the sexual compatibility of the thalli, and it has been shown that segregation of this factor probably takes place in a 1 : 1 ratio. There is no sex segregation, however, for both the microconidia and the receptive bodies consistently develop on each thallus, irrespective of whether these have arisen from single ascospores or from single hyphal tips. The term heterothallism in Blakelee's sense cannot, therefore, be applied to the phenomenon found in *S. Gladioli*.

Miss Cayley (**6**) points out that sex heterothallism is only one of several forms of heterothallism, and that it is perhaps due to the confusion of these various types that the theory of multiple sexes has gained such a hold. The conception of sterility as the controlling factor in cases similar to the one under discussion was suggested by Brunswik (**5**), who postulates the existence of two sexes only, the interactions between them being controlled by one or more factors other than those of sex, *i.e.* negative sterility factors. In connection with a discussion of the observations on *Humaria granulata,* Miss Cayley (l. c.) states, " The mycelia must be self-sterile, and although haploid, must be potentially bisexual. They fall into two definite groups in the ratio of 1 : 1, and the members of each group are sterile *inter se*. . . . This is not sex heterothallism, but a form of physiological heterothallism based on one self-sterility factor in a haplo-synoecious fungus." This expresses exactly the interpretation here placed on the situation in *S. Gladioli*.

SUMMARY

Efforts to obtain a sexually formed fruiting body from the minute sclerotia formed by the fungus previously known as *Sclerotium Gladioli* Massey were unsuccessful. Similar trials with the stromatic tissue led to the discovery of structures which proved to be receptive in character, for when these were spermatized with

microconidia from certain other thalli, they developed apothecia of the *Sclerotinia* type.

Monomycelial cultures develop both receptive bodies and microconidia, and ten isolates thus derived from various localities and suscepts were crossed in all possible ways and the development or lack of development of apothecia in the various crosses was tabulated. This experiment demonstrated the fact that the isolates used could be divided into two groups on the basis of compatibility, and these exhibit intra-group sterility, inter-group fertility, and individual self-sterility.

Single ascospore cultures were made, the receptive bodies from these were back-crossed separately with microconidia from each of the parent isolates, and this showed clearly a segregation of the compatibility factor, apparently in the ratio of 1 : 1.

Other experiments demonstrated that receptive bodies could be fertilized by microconidia developing on ascospores which had been discharged on the receptive bodies; that a filtered suspension of microconidia in which the latter were removed, did not effect fertilization, and that apothecia would not develop as the result of hyphal fusions, even between compatible isolates.

Optimum cultural conditions for the development of microconidia and receptive bodies are outlined, and also the technique used for the process of spermatization and the development of the apothecia. Experiments were performed which demonstrated that the receptive bodies are the only structures capable of fertilization by the microconidia.

Some preliminary cytological notes are given, including details of the changes which take place in the coiled ascogonial hyphae of the receptive bodies, when the later are spermatized with compatible microconidia.

Some speculation is made on the operation of this sexual mechanism in nature, for the microconidia, receptive bodies, and apothecia have been seen only in artificial cultures.

The phenomenon exhibited by this sexual mechanism is not regarded as one of heterothallism, as Blakeslee defined this term, for there is no segregation of the sexes in separate thalli, but rather a homothallic condition in which each thallus is self-sterile and fertility exhibited only between certain compatible thalli.

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EXPLANATION OF PLATES

PLATE 5

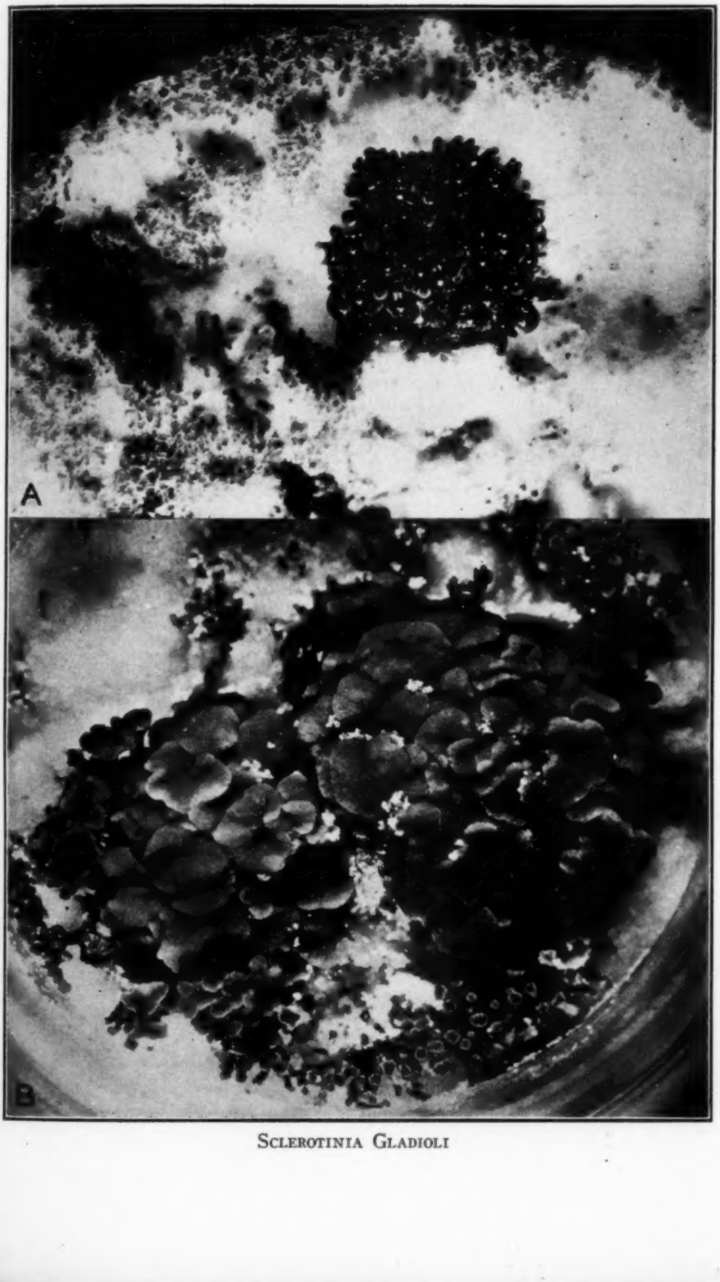
A, The crocus isolate growing on a sterilized gladiolus corm. Receptive bodies have formed and two groups (one only showing) have been spermatized with compatible microconidia. Note the apothecial fundaments developing in the spermatized area; the remaining receptive bodies continuing unchanged, $\times 4$; *B,* a larger area of the culture shown in *A,* three weeks later. The apothecia from the spermatized groups are now mature. The originally unspermatized receptive bodies, now spermatized by microconidia formed by the ascospores shot from the previously matured apothecia, are forming apothecia, $\times 3$.

PLATE 6

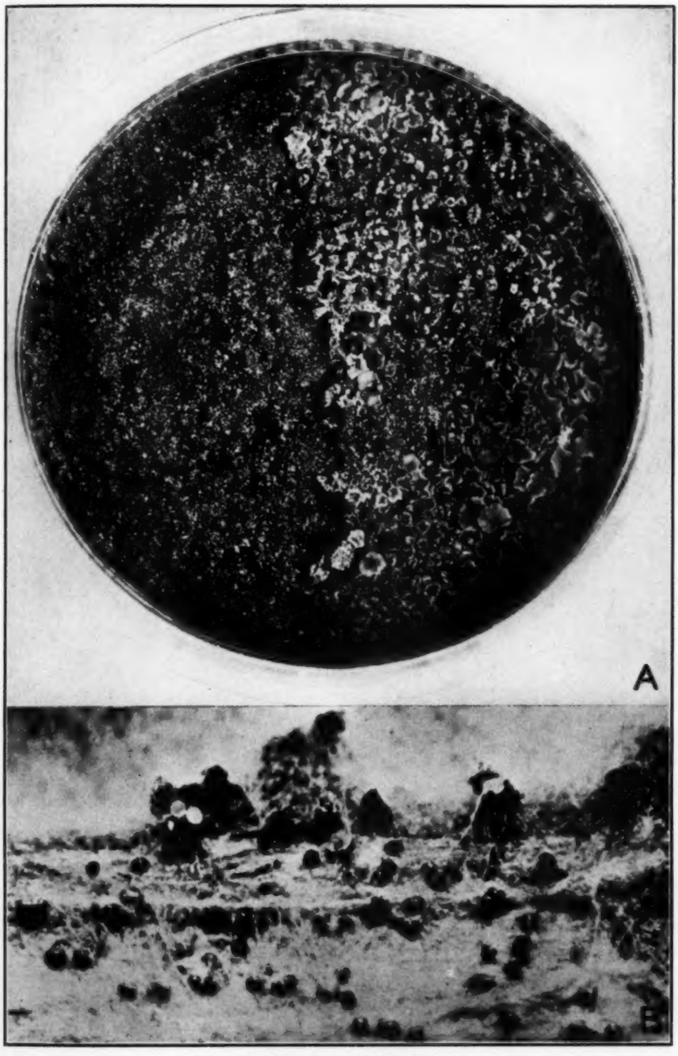
A, A test culture in a Petri dish, the right half spermatized with compatible microconidia, the left half treated with soil extract alone, natural size; *B,* A six weeks old *Lycium* stem-potato-dextrose agar culture. Note the sclerotia in the foreground, and three receptive bodies in the background with microconidial sporodochia formed on them, $\times 8$.

PLATE 7

A, A longitudinal section of a receptive body, showing the stromatic base and part of its rind, the pilose exterior, the sterile apical hyphae, and the central system of coiled ascogonial hyphae, $\times 70$; *B,* The apex enlarged to show the overarching of the sterile hyphae and the depression formed at the center, $\times 210$; *C,* Part of the coiled ascogonial system showing the intricacy of the coiling, $\times 2000$; *D,* Section through portion of a coil showing their deep staining character and the nuclei, $\times 2250$; *E,* Section through the stroma, showing the loose structure of the rind, and the coiled ascogonial hyphae beneath the surface prior to the development of a receptive body, $\times 1000$.



SCLEROTINIA GLADIOLI



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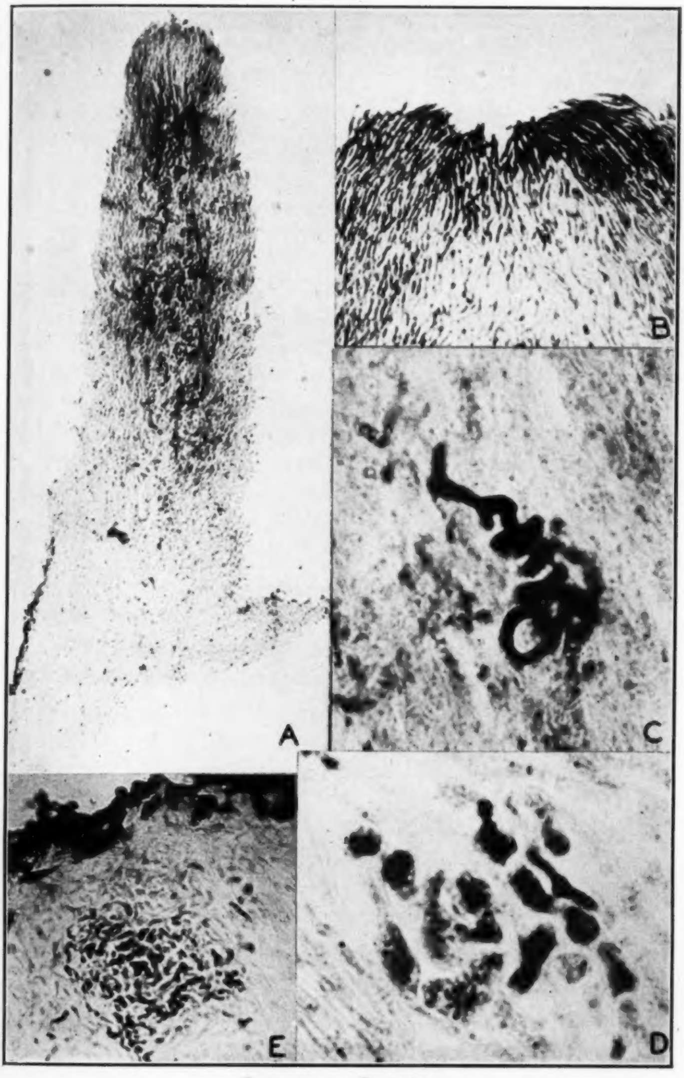

SCLEROTINIA GLADIOLI

DASYSCYPHAE ON CONIFERS IN NORTH AMERICA. I. THE LARGE-SPORED, WHITE-EXCIPLED SPECIES

Glenn Gardner Hahn and Theodore T. Ayers

(with plates 8–13)

INTRODUCTION

With the discovery of the European larch canker on introduced *Larix europaea* D.C. in Massachusetts in 1927, and the subsequent diagnosis of the introduced causal organism as *Dasyscypha calycinia* (Schum.) Fuckel by Spaulding and Siggers (following general British usage) (**13**), extensive scouting for the disease was performed to determine whether the parasite was widely distributed. A pathological investigation of the disease was also undertaken particularly with reference to the host relationships of the causal fungus.

On account of the considerable nomenclatorial confusion in the literature brought about by the variety of names which had been applied in Europe to the larch canker parasite since the middle of the 19th Century, there immediately arose the pressing mycological problem, in this case of particular economic concern, having to do with the exact morphological determination of the larch canker organism. This confusion was increased by the fact that in North America the European parasite had been identified as being present previous to the actual discovery of typical cankers on imported larch in this country. It therefore became necessary to recognize this organism in order that its presence and spread in this country on larch and other conifers might be determined with a high degree of certainty. The fact that in Europe the parasite had been reported on pine and Douglas fir, caused considerable concern when related *Dasyscypha* forms were discovered (**7**) on cankered Douglas fir [*Pseudotsuga taxifolia* (LaM.) Brit., blue form] in New England. These diseased Douglas firs in certain instances were growing in close association with the imported larch. Ac-

cordingly it became highly important to ascertain whether the imported parasite constituted a potential menace to Douglas fir in this country.

The extensive scouting for the disease among conifers in New England and the Middle West produced numerous collections of *Dasyscypha*. These were augmented by other collections taken in the South and on the Pacific Coast. The authors were thus able to study morphologically and culturally a comparatively large number of forms collected throughout the United States and in Canada.

In addition to collections of the European larch canker organism, fresh material of the following coniferous parasites were made available for study: *Dasyscypha fuscosanguinea* Rehm, *D. resinaria* (Cooke & Phil.) Rehm, *D. Ellisiana* (Rehm) Sacc. (the newly discovered parasite of Douglas fir), and *Dasyscypha* forms nearly related to *D. calyciformis* (Willd.) Rehm.

It is the purpose of the writers to publish their observations on North American *Dasyscyphae* on conifers in a series of papers of which the present one is the first. In this publication the large-spored, white-excipled forms are dealt with. The native species are differentiated from the economically important introduced parasite, *Dasyscypha Willkommii* (Hartig) Rehm, (the Continental name for the European larch canker fungus, accepted by the authors), and the European saprophyte, *D. calycina*. Pathological data used to corroborate physiological differences among the species studied, are only briefly alluded to, and will be reported in detail elsewhere.

THE GENUS DASYSCYPHA

The taxonomy of *Dasyscypha* (1869) has been the subject of controversy due to the acceptance of Karsten's genus, *Lachnum* (1871). Adhering to priority of position as published, *Dasyscypha* Fuckel (**2**)with its type, *D. bicolor* (Bull.) Fuckel, which was the first species described under the new genus, should replace *Lachnum* Karst. (**8**), containing species with paraphyses "apice acutae vel acutatae aut saltem attenuatae, discretae." *D. bicolor* is recognized as having broad, acerose paraphyses. Unfortunately when Fuckel raised the Friesian (Syst. Myc. **2**: 89,

1822) tribal name, "Dasyscyphae" (δασύς, hairy; σκύφος, a cup), of the large genus *Peziza,* to generic rank, he briefly described his new genus without mentioning the morphological characters of the paraphyses. Of the seven species listed by Fuckel under his new genus, only one, *D. calycina,* had filamentous paraphyses. For reasons outlined above, Boudier (Bull. Soc. Myc. Fr. **1**: 117. 1885) reserved the Fuckelian name, *Dasyscypha,* for the hairy-stalked forms with broad, lance-shaped paraphyses, wherein he placed *D. bicolor* and *D. cerina* (Pers.) Fuckel, whereas *D. calycina* was referred to his new genus, *Trichoscypha.*

Fuckel's genus *Dasyscypha* was recently discussed by Nannfeldt (**9**, pp. 298–299) who, although he admitted the priority claim of *Dasyscypha,* believed that the retention of Fuckel's genus for species with filamentous paraphyses would only lead to confusion. Accordingly he would retain the distinct generic name *Lachnum* of Retzius (Fl. Scand. Prodr. 329. 1779), and of Karsten (**8**), for forms with lanciform paraphyses, and do away entirely with the name *Dasyscypha.* Since Nannfeldt found that *Trichoscypha* of Boudier was a homonym of the older *Trichoscypha* Hook., he substituted his new name, *Trichoscyphella* [*T. Willkommii* (Hartig) Nannf.].

The confusion which Nannfeldt would avoid appears to be added to by this procedure in discarding *Dasyscypha.* It is not the purpose of the authors to argue the point. They are of the opinion that because of the long-time usage of *Dasyscypha* and the universal recognition of the genus, it should be retained. Following Rehm, and Clements and Shear (The Genera of Fungi. 1931), they have allocated to *Dasyscypha* the hairy-cup coniferous Discomycetes, all of which were found to have filamentous paraphyses, with extremities unswollen, obtuse or subacute, or slightly swollen. It is here suggested, however, that inasmuch as the pre-Friesian genus, *Lachnum* Retz., accepted by Rehm and others, has been employed to indicate forms having lance-shaped, "vulgo grandiusculae" paraphyses (**8**), it would seem proper to accept Fuckel's second-named species, *D. calycina,* as the type of *Dasyscypha.*

There has been considerable discussion over the identity of Fuckel's *Dasyscypha calycina* (Schum.) and its relationship to

Peziza calycina Schum. and *P. calycina* Fries. For reasons given in the following section the Fuckelian species is upheld.

HISTORY AND DESCRIPTION OF DASYSCYPHA CALYCINA

When Fries (1822) introduced the tribe "Dasyscyphae" he included the species *Peziza calycina* despite the fact that Schumacher (Enum. Pl. Saell. **2**: 424. 1803) had previously occupied that name with a Discomycete collected "in strobylo *Pini abietis.*" Fries described three forms of his species:

α. *Pini sylvestris* (Syst. Myc. **2**: 91, 1822) = *P. calyciformis* Willd.; *P. calycina* Schum., "in ramis *Pini silvestris.*"
β. *Abietis*
γ. *Laricis* (Elench. Fung. **2**: 8. 1828) "in ramis, *Pini laricis,* Chaillet."

The description of the first-named form, *Pini sylvestris,* which was given in greater detail than the others, is nevertheless inadequate in revealing to us just what fungus on pine Fries actually intended. Undoubtedly he was dealing with a heterogeneous group of fungi on pine, fir and larch. His first form, *Pini sylvestris,* may or may not have been *D. calyciformis* (Willd.) Rehm with short, elliptical spores. Because of the common occurrence of this saprophyte in Europe on pine, spruce and fir, it is quite possible that Fries was concerned with this fungus but of this we are not sure. No spore measurements were given by him or by Schumacher for his fungus, the type of which is now known to be lost.

In 1869 Fuckel (**2**) definitely occupied the name *Dasyscypha calycina* with a large-spored fungus "an dürren berindeten Aesten von *Larix europaea*" for which he was the first to give spore measurements. It is not at all probable that his fungus was the same as Schumacher's on fir cones; for the large-spored *Dasyscyphae,* as this paper will show, are extremely limited in their host range.

It is a convention among mycologists to accept Fries' names for Ascomycetes where these are sufficiently described. Where a species is insufficiently delineated it has been the custom to take the name given by the first investigator after him who gave a description on which a species could be based. Fuckel was the first after

Fries to adequately occupy the name, *Dasyscypha calycina* with a fungus, which from his description, we can consider saprophytic on larch.

Opportunity was afforded to examine a herbarium specimen, Fungi Rhen. *1206, D. calycina* Fuckel, from the Herbier Barbey-Boissier at Geneva (PLATE 8, FIG. 1). This collection, which was issued by Fuckel in 1864 previous to the publication of his original description (**2**), was acquired in 1894 by Barbey-Boissier after Fuckel's death (1894), and distributed by them. The Geneva specimen contained abundant ascocarps and these, although considerably weathered by long-keeping, showed spores agreeing in size with those described by Fuckel.

An amended description of *D. calycina* which follows, attempts to clearly define that species. In doing so, we hope to terminate the controversy over the relationship between this saprophyte, which we found to be non-pathogenic, and the parasite of Berkeley, Willkomm and Hartig. Our evidence supports in part the Continental school who have maintained, contrary to the British point of view,[1] *D. Willkommii* to be a distinct species. It does not support, however, the Continental usage of Fries' name "*calycina*" to designate a short-spored *Dasyscypha* on pine and other coniferous hosts, for the reason that the name "*calycina*," as we have endeavored to demonstrate, is definitely occupied by a much larger-spored fungus which Fuckel intended, on larch.

DASYSCYPHA CALYCINA Fuckel Symb. Myc. 305. 1869. **Descr.** emend. nec *Peziza calycina* Schum. Enum. Pl. Saell. **2**: 424. 1803.

Ascocarps abundant, solitary or grouped, with short stalks, erumpent, at first globular, closed, opening in a rounded form, and

[1] What may be called the British contention is that *Dasyscypha calycina* (Schum.) Fuckel is the proper name by which the European larch canker parasite should be recognized (**6**). However, this view has not been held by all British workers, *e.g.*, H. M. Ward (Timber and some of its diseases *227–243.* 1889) was of the following opinion: "At the margins of the flattened patch, just where the dead cortex joins the normal living parts, there may frequently be seen a number of small cup-like fungus fructifications, each of which is white or grey on the outside, and lined with orange-yellow. These are the fruit bodies of a discomycetous fungus called *Peziza willkommii* (Hartig), and which has at various times, and by various observers, received at least four other names, which we may neglect."

expanding with humid conditions to a flattened, saucer-like structure with a comparatively thin rim (PLATE 8, FIG. 2); externally whitish with cylindrical, thin-walled hairs, minutely roughened, with gently rounded, slightly swollen extremities, septated, cells short, 3–4 μ broad, hairs persistent (PLATE 9, FIG. 8), disc ochraceous-salmon[2] to salmon-orange 0.5–3 mm. diam; asci clavate, frequently swollen toward the apex with obtusely-rounded apices, range (198) 82.8–165.6 × 6.8–12.8 μ, commonly, 100–130 × 8–10 μ (PLATE 9, FIG. 6). Ascospores eight, uniseriate, continuous at first, commonly uniseptate upon germination, smooth, hyaline, elongate-elliptic or elliptic-oblong, very rarely fusiform or pointed at one end, range (340) 12.6–21.4 × 4.2–8.4 μ, commonly, 14–19 × 5–7 μ (PLATE 9, FIG. 7); paraphyses outranking asci, variable, slender, filamentous, unswollen at the extremities, commonly intermixed with broader filaments, irregularly submoniliform, with swellings near their extremities, obtusely rounded or attenuate with subacute apices, occasionally spathulate, septate, range (155) 90–180 × 1–4 μ (PLATE 9, FIG. 6).

Imperfect stage consisting of erumpent, fleshy, waxy stromata containing simple or labyrinthiform loculi in which microconidia (spermatia) are abstricted from the tips of short, subulate sporophores, simple or verticillately-branched (PLATE 9, FIG. 9); microconidia continuous, hyaline, elliptic-oblong or allantoid (100) 2–5 × 1–2 μ (PLATE 9, FIG. 10). Germination not observed.

Type—Fungi Rhen. *1206.* (Barbey-Boissier, Herbier Boissier *1316,* Geneva.)

The fungus has been observed as a saprophyte in Massachusetts where the European larch canker parasite was introduced. The following collections from the Matthews Estate, Hamilton, Mass., made in 1929–1931 have been studied.[3]

On *Larix europaea.*—*43536,* coll. G. G. Hahn & J. R. Hansbrough; *43561–62,* coll. H. Metcalf, P. Spaulding, N. O. Howard & Hahn; *43564–65,* coll. Hahn; *53057,* coll. Hahn, T. T. Ayers & C. S. Moses; *53067,* coll. Ayers; *53131,* coll. Hahn; *53701,* coll. Hahn & Ayers.

On *Larix leptolepis* Gordon.—*53087,* coll. Hahn; *53702,* coll. Hahn & Ayers.

On *Pseudotsuga taxifolia,* blue form,—*53056,* coll. Ayers. An

[2] The color nomenclature used is that of R. Ridgway, Color standards and color nomenclature, 1912, Washington, D. C.

[3] Unless otherwise indicated, collection numbers denote specimens for study filed in the Division of Forest Pathology, New Haven, Conn.

intensive search in 1930–1932 showed that *D. calycina* was exceedingly rare on this host. Previously on July 17, 1927, Siggers (**13**) found a scant collection (*53883*) of the species occurring saprophytically on a twig of blue Douglas fir growing in the Hamilton, Mass. area. A mono-ascus strain of *D. calycina* isolated from the Douglas fir collection, *53056,* and inoculated into a dying blue Douglas fir (August 13, 1931) produced numerous apothecia (1933) about the incision, the paraphyses of which were submoniliform (PLATE 9, FIG. 6), being characteristic of those recognized as typical for the species.

In Scotland the senior author found *D. calycina* occurring occasionally as a saprophyte on the green form of Douglas fir growing in a mixed planting with badly diseased European larch. Despite the crowded condition of the stand on a site favorable to the development of larch canker, it was observed that the Douglas fir was not affected by the larch canker organism (*D. Willkommii*). However, collections of *D. calycina* were made on both *L. europaea* and *Pseudotsuga taxifolia.*

Ascocarps of *D. calycina* on Douglas fir in Scotland collected during the spring and summer (1927 and 1929) on weakened, partly living, or dead Douglas fir branches and twigs, were never so abundant as those found upon larch. The following Scottish collections were made at Glentress, Peeblesshire: *43510–33–34, 43998.*

Scottish examples of the fungus have also been identified in the herbarium of Dr. J. S. Boyce, among them: *1607, Larix eurolepis* Henry, and *1606, L. europaea,* Dunkeld, coll. J. S. Boyce, Aug. 11, 1925; *1603, Pseudotsuga taxifolia,* Bowmont near Kelso, coll. J. S. B., Aug. 19, 1925.

Among fresh specimens of *D. calycina* on *Larix europaea* which have been studied from Great Britain and the Continent are the following: *43500–6–7–20,* Glentress, Peeblesshire, Scotland, coll. Hahn, June, 1929; *53128,* Yorebridge, Scotland, coll. M. J. F. Gregor, Feb. 7, 1931; *53130,* Hann.-Münden, coll. E. Plassmann, Sept. 1930; *53158* (on upper edge of canker in which *D. Willkommii 53159* was fruiting), West Linton, Scotland, coll. Gregor, May 3, 1931; 53811, Forêt du Rac Estable, Axat, Aude, France, coll. G. Fenwick-Owen & G. D. Darker (*3956*) Mar. 2, 1932;

53829, Zürichberg, Zurich, coll. G. D. D. (*4093*) June 15, 1932; *53836,* Nový Smokovee, Czechoslovakia, coll. G. D. D. (*4187*) July 18, 1932; *53837,* Vimperk (Winterberg), Czechoslovakia, coll. G. D. D. (*4136*) July 2, 1932.

Exsiccata examined:

Fungi Rhen. *1206, Dasyscypha calycina* (Schum.) Fuckel. (Herb. Kew) is without apothecia.

Fungi Rhen. *1206, D. calycina* (Schum.) Fuckel. 1864 (Herb. Bot. Mus. Berlin—" sehr spärliches Material " according to a written communication from Dr. Ulbrich) is neither *D. calycina* nor *D. Willkommii,* but a closely related form with blunt, elliptic spores, 11–17 × 5.5–7 μ and fine filamentous paraphyses mostly unswollen or very slightly so at the tip. The ascocarps are quite minute.

Fungi Rhen. *1206, Dasyscypha* (*Peziza*) *calycina* (Schum.) Fuckel. 1864 (Farlow Herb.) is possibly identical with the Berlin specimen. The material is exceedingly meagre and weathered, spores 12–16 × 4–5.5 μ and filamentous paraphyses mostly unswollen at the tip. Fungi Rhen. *1206, 1864* (*1316,* Barb. Bois., 1894), from the same herbarium, is a small-spored form, 5–8.5 μ long belonging to the *D. calyciformis* (Willd.) Rehm group.

Fungi Rhen. *1206, D. calycina* (Schum.) Fuckel. 1864 (*1316,* Herb. Bois., 1894) in Myc. Herb., U. S. D. A., Washington, D. C., is also exceedingly meagre. Slides of one ascocarp did not reveal any morphological detail. A slide of a second ascocarp prepared in 1928 by W. W. Diehl showed only a very few elongate-elliptic spores, several of which were fusiform, 14–21 × 5–7 μ, associated with filamentous, unswollen paraphyses. Although apparently closely related, it is probably not *D. calycina* because of the absence of the submoniliform paraphyses.

We were very fortunate in obtaining the Geneva material for the foregoing studies of the type *D. calycina.* In our search for type material of *D. Willkommii* we were not so fortunate. Our observations on this species have been made largely from fresh European and American material.

HISTORY AND DESCRIPTION OF DASYSCYPHA WILLKOMMII

The European larch was introduced into the lowlands of Germany from its native habitat about the beginning of the 18th Century. There it appeared to thrive successfully in artificial plantations. About the middle of the following century there appeared a serious canker disease among the planted larch, which in certain areas caused considerable damage by deforming and killing young stock.

For a hundred years there occurred continual strife in the literature as to the cause of the larch canker. At first the articles on the disease were largely pathological in nature. It was Hiley (**6**) who pointed out that in 1859 Berkeley (Gard. Chron. 1015–1016) was the first to ascribe the cause of the canker to a fungus. In a specimen, "forwarded by Sir Walter C. Trevelyan," Berkeley found that "mycelium has penetrated through the bark and produced its proper fungus, under the form of *Peziza calycina.*" He went on to relate that, "In a small plantation, most of the trees of which are young, nearly all are more or less attacked on stem or branch with the *Peziza.*" Seven years later Willkomm (**14**) published his treatise setting forth in great detail the symptoms and etiology of the disease and ascribed the cause to a Discomycete which he profusely illustrated but incorrectly called *Corticium amorphum* (Pers.) Fries. He came by this error as the result of blindly accepting a determination of the European larch canker organism as *C. amorphum.* This determination had been made by Rabenhorst apparently in haste and without critical observation. It is a well-known fact that this Basidiomycete superficially resembles certain *Dasyscypha* forms to such an extent that they can be readily confused, *e.g.*, a specimen of *Peziza calycina* Fries *β abietis,* Fungi Rhen. *2192,* 1868, in the Farlow Herbarium, Harvard University, is not a *Dasyscypha* but *Aleurodiscus amorphus* (Pers.) Rabenh. (*Corticium amorphum*).

Hoffman (Forst-u. Jagd-Zeit., May, 1868) corrected Willkomm's error and adopted the same name for the fungus as Berkeley. Robert Hartig (**4**) likewise recognized Willkomm's mistake, but in correcting the error he made a new name, *Peziza Willkommii* Hartig in honor of the forest pathologist, Willkomm, for he believed the larch canker parasite to be a new species. In

commenting upon the correction made by Hoffman, which Hartig regarded as an error, he stated that among the varieties of *P. calycina* based upon host differences as established by Fries, he (Hartig) recognized well-defined differential characters in the size and shape of the ascospores and the size of the asci and paraphyses. In the case of *P. calycina* Fries, Hartig understood a short-spored form on pine and fir, that was probably identical with *Dasyscypha* (*Peziza*) *calyciformis*, the species recognized not only by Rehm but also by mycologists of the present day. Hartig added very little to the morphological detail of the larch parasite. As in the case of Willkomm, he was largely concerned with the disease caused by the organism and in his brief description Hartig referred to the morphological data given in Willkomm's paper. He (**5**) illustrated a fungus with large, elliptic-fusiform spores and filamentous paraphyses, unswollen at their apices. Apparently neither Willkomm nor Hartig distinguished between the parasitic and saprophytic forms on larch. There is no doubt, however, that they were largely concerned with the fungus fruiting "besonders an Krebstellen" (**4**, **5**), which was causing so much discussion at that time.

In 1889 Saccardo (Syll. Fung. **8**: 437) placed Hartig's new fungus as a synonym of *Dasyscypha calycina* Fuckel. He described a form with large spores and filiform paraphyses "sursum incrassatulis," occurring on larch and Scotch pine in Britain, Germany, France and Italy. Saccardo did not mention the presence of elongate-fusiform pointed ascospores.

Rehm in 1871 issued a specimen (Rehm, Ascom. *62*), *Dasyscypha calycina* (Schum.) Fuckel, collected by himself. Linhart referred to this collection when in 1882 he issued Fungi Hung. *62*, to which he applied the combination, *Dasyscypha Willkommii* (Hartig) Rehm.

Carruthers (**1**) in 1891 used this same binomial independently for the organism causing canker of the larch. In an exceedingly comprehensive paper dealing largely with the disease, Carruthers stated: "The structural characteristics are no doubt sufficient to separate this fungus (the hitherto unnamed plant figured by Willkomm which Hartig designated as *Peziza Willkommii*) as a distinct species, apart from the consideration that it attacks only the

living larch, while the *Dasyscypha calycina* is found on the dead branches of the Scotch fir . . . the plant must now be called *Dasyscypha Willkommii.*" Carruthers, judging from statements made concerning his pathological observations, was firmly of the opinion that the larch canker fungus was essentially a parasite of very young active bark, which it was able to penetrate causing fresh cankers by new and independent attacks. He figured a fungus with large, elliptical spores associated with filamentous paraphyses unswollen at the tip. Without a doubt Carruthers was concerned with the true larch canker parasite despite the fact that he failed to note the pointed spores which are so characteristic of the parasite. He regarded *D. calycina* as quite a distinct species on pine.

In 1896 Rehm (**12**) published the first complete description of *D. Willkommii* (Hartig) with illustrations of a large-spored form with elongate-elliptical and spindle-shaped, pointed spores, associated with filamentous paraphyses unswollen at the tip as figured by Hartig (**5**). Rehm erred, however, in regarding *D. calycina* Fuckel (Fungi Rhen. *1206*) as a synonym, showing the general tendency of the time not to recognize specifically a closely related but distinct, large-spored saprophytic form.

A preliminary study in the field and laboratory in Scotland in 1929 convinced the senior author that the European larch canker organism could be distinguished morphologically and physiologically from nearly related saprophytic forms. A continuation of this study among diseased imported larches in the United States showed conclusively that the imported parasite was a distinct species.

[4] The variety *Fuckelii* Bresad.,—syn. *Dasyscypha calycina* var. *minor* Rehm (Ascom. Lojk. 8, 1882), of *D. Willkommii* was proposed by Rehm anew in 1896 (**12**, p. 833) for a specimen in his herbarium. He described this varietal form as follows: "Schläuche cylindrisch, 90–100 μ long, 7–8 μ breit. Sporen elliptisch, stumpf, 10–15 μ long, 5–6 μ breit. An dürren Aesten von Lärchen . . . (Bres.), von *Pinus pumilio* . . . (Britzelmayr), . . . Bresadola bezeichnete seinen Pilz als synonym zu *Dasyscypha calycina* Fuckel, nec Schum. Derselbe ist aber doch nur als kleinsporige Form von *D. Willkommii.* . . ." Previously Bresadola commented upon a small-spored fungus, *Dasyscypha calicina* (Hedw.) Fries, (Roum. Rev. Myc. **13**: pt. 49, 23, 1891), "sur les branches de l'*Abies excelsa*," but he did not mention a variety *Fuckelii.* Until the authors have examined Rehm's specimen in order to determine the character of its paraphyses which he did not de-

The following description of *D. Willkommii* will serve to separate the parasite from the nearly related large-spored saprophyte *D. calycina.*

DASYSCYPHA WILLKOMMII (Hartig) Rehm in Ber. Naturh. Ver. Augsburg **26**: 19. 1881; Rab. Krypt.-Fl. **1**^{3}: 832. 1896.[4] Syn. *Peziza Willkommii* Hartig.

Trichoscyphella Willkommii (Hartig) Nannfeldt.

Apothecia very robust (PLATE 10, FIGS. 2, 3), waxy, fleshy, scattered or grouped, erumpent, at first globular and closed, then opening urn-like and expanding saucer-shape, disc bulging in a convex manner forming a convoluted hymenial surface with an irregular periphery; rim not becoming laterally compressed on drying, comparatively thick and splitting in a cruciform manner under moist conditions; short but distinctly stipitate; externally chalky-white (PLATE 10, FIG. 2), covered densely with excipular hairs, minutely roughened, hyaline, thin-walled, cylindrical with slightly swollen, gently-rounded extremities, septated, forming short cells, 3–4 μ broad, persistent (PLATE 9, FIG. 3); disc apricot-orange or apricot-buff to salmon-buff fading to light buff, 3–6 mm. diameter. Asci clavate, apex obtusely rounded, range (205) 126.0–172.8 × 9.0–14.0 μ, commonly, 140–162 × 10–13 μ (PLATE 9, FIG. 1). Ascospores eight, obliquely uniseriate, hyaline, smooth, continuous at first commonly uniseptate upon germination, elongate-elliptical, fusiform, obtuse or acute extremities, or acute at one end, range (200) 15.6–27.8 × 6.0–9.4 μ, commonly, 17–25 × 7–9 μ (PLATE 9, FIG. 2). Paraphyses outranking asci, flexuous-filiform, generally not swollen toward the tip, or only very slightly so, with obtuse extremities, septate, range (50) 158.4–216.0 × 1–3 μ, extremities 1–4 μ broad (PLATE 9, FIG. 1).

The conidial which precedes the apothecial stage consists of waxy, fleshy, erumpent, whitish stromata with irregular labyrinthiform cavities in which the microconidia (spermatia) are abstricted from the tips of slender, subulate, acutely-pointed, simple or verticiallately-branched sporophores (PLATE 9, FIG. 4); microcondidia (PLATE 9, FIG. 5), hyaline, continuous, elliptic-oblong, or allantoid, with obtuse extremities, (100) 2–8 × 1–2 μ [Hartig (**5**) *pl. 11, fig. 16, 17, 18;* Plassmann (**10**, p. 14) fig. 5; Gaisberg (**3**), *pl. V, fig. 13, 14*]. Germination was tested repeatedly but was unsuccessful.

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scribe, and have compared cultures made from fresh collections of this European variety, they cannot state whether it is identical with their new North American species, *D. occidentalis.* Further study may show the European variety to be a distinct species.

Dasyscypha Willkommii is only to be found in immediate association with the lesions (PLATE 10, FIG. 1) which it causes. Later *D. calycina,* among other saprophytes, may come in about the canker after the vigor of the branch part attacked, has greatly declined or the branch is dead, spreading prolifically throughout the dead tissue.

Numerous specimens of the typical European larch canker organism have been collected (1927–1931) by members of the Division of Forest Pathology on *Larix europaea* which host was introduced from Great Britain into Massachusetts upon the Palmer Estate, Ipswich, and the Matthews Estate, Hamilton, in a diseased condition.

The organism was also found fruiting very sparsely upon lightly cankered *Larix leptolepis* which was also imported from Great Britain.

The senior author made numerous collections of typical *D. Willkommii* in Scotland and Norway which agree morphologically with specimens collected in the United States. A specimen of the fungus collected on *L. europaea* at Weissenbach, Austria, by Dr. E. P. Meinecke, July 16, 1914 (Herb. E. P. M.) was found to be identical with the American material.

D. Willkommii is reported to cause larch canker not only upon *L. europaea* and *L. leptolepis,* but also upon *L. occidentalis* Nutt., *L. sibirica* Led., *L. laricina* (Du Roi) Koch, and *L. dahurica* Turcz. in Europe. The authors have been able to infect artificially *L. laricina, L. europaea* and *L. leptolepis* with the fungus in the United States. Spaulding in a verbal communication stated that in May, 1922, he observed both the native American larches, *L. laricina* and *L. occidentalis,* infected with the European larch canker disease in Bagley Wood, England.

Exsiccata examined:

An effort was made to secure some of Hartig's original material of *Peziza Willkommii.* Through the kindness of Dr. Mary J. F. Gregor, Edinburgh, Scotland, information was obtained from Dr. K. von Tubeuf concerning type material of *D. Willkommii* collected by Hartig at the time of his first description. It was, however, not possible to obtain material for study of this period for reasons stated by Tubeuf in correspondence,—" . . . Die 1 Bes-

chreibung Hartigs (Wichtige Krankheiten der Waldbäume) ist in Eberswalde bei Berlin gemacht vor 1879. Diese Sammlung ist grösstenteils oder ganz zur Zeit Brefelds durch Annobien zerstört worden."

Rehm, Ascom. *62b, Dasyscypha Willkommii,* coll. J. Rick, 1898 (at Farlow Herb.) appears to be the larch canker parasite; Rehm, Ascom. *62b, D. Willkommii* Hartig, coll. Magnus, 1892 (at Farlow Herb.) is not *D. Willkommii* but a related large spore form. The paraphyses appeared to be swollen at the tips but these were so degenerate that it was impossible to tell much about them.

Kunze, Fungi Sel. *383, D. Willkommii* (Hartig) Winter,—syn. *Peziza Willkommii* Hart., coll. G. Winter, *1878* (Farlow Herb.) is neither *D. Willkommii* nor *D. calycina,* but a distinct form.

Linhart, Fungi Hung. *62, D. Willkommii* (Hartig), cfr. Rehm, Ascom. *62, Peziza Willkommii* Hartig, 1882 (Herb. E. P. Meinecke) does not appear to be *D. Willkommii* but possibly *D. calycina.* The rather poor, large-spore material showed comparatively broad paraphyses, some of which were swollen toward the tip.

TWO UNDESCRIBED NORTH AMERICAN DASYSCYPHA SPECIES

Both *Dasyscypha calycina* and *D. Willkommii* have been reported by mycologists as occurring in North America before these two European species were actually demonstrated as being present on imported larch. Kauffman (Unreported Michigan Fungi for 1909, Rept. Mich. Acad. Sci. **12**: 99–103. 1910) recorded *D. Willkommii* on fallen twigs of *Larix* in a tamarack bog. In a letter to G. Hamilton Martin, May 28, 1921, Kauffman stated, ". . . I have a collection of what I report as *Dasyscypha Willkommii* Hartig and have never had a critical survey of our tamarack to study its actual effects. I should say off-hand that no serious effect is due to it in the bog swamps of Michigan." Kauffman again reported the fungus from New York State (Bull. N. Y. State Mus. **179**: 80–104. 1915) on twigs of American larch. Again in 1911, Güssow reported *D. Willkommii* Hartig from Nova Scotia (Rep. Dom. Bot. year ending Mar. 1911, p. 259). In a letter to the senior author, June 10, 1931, Güssow commented as follows: " I may say that later evidence revealed that the fungus

reported was not *Dasyscypha Willkommii,* the cause of larch canker, but a related species of no special importance. We have been on the lookout for *D. Willkommii* ever since, but have not found any evidence in Canada."

J. R. Weir in correspondence with A. H. Graves, August 1, 1917, discussed the large-spored *Dasyscypha* forms which he had under observation in the western United States. Quoting in part from his letter he was of the following opinion: "There is absolutely no difference between *Dasyscypha calycina* (Schum.) Fuckel and *D. Willkommii* Hartig. At least, so far as I have ever been able to determine from the examination of material under both names from various parts of Europe and America. . . . The fungus is very common throughout western United States and Canada but I do not consider it of much economic importance. I have found it fruiting in wounds of branches and stems of young trees but it never seems to produce the cankers so much described in European literature. . . . The fungus is usually found fruiting on old fallen twigs and branches. I occasionally find it fruiting on branches of old living mistletoe brooms, which indicates a slow parasitic action. The fact that our American plant does not seem to behave in the same manner as the European plant rather indicates a different form or that we do not have the true *D. Willkommii.* The varieties of *D. calycina,* viz. *Laricis* seems to be nothing more than the true form on different hosts. I find it on *Picea, Larix* and *Abies.*" It is here interesting to note that Sydow and Petrak (Ann. Myc. **20**: 178–218. 1922) later identified *Dasyscypha* specimens on branches of *Larix occidentalis* from Idaho as *D. Willkommii.*

In his manual of economic plant diseases new to or not widely distributed in the United States, J. A. Stevenson (Foreign Plant Diseases, p. 99, U. S. Dept. Agr. 1926) listed the European larch canker parasite *Dasyscypha calycina* (Schum.) Fuckel (*D. Willkommii* Hartig). Stevenson stated that the organism had been reported from Newfoundland and commented upon the possibility of its introduction into the United States. The following hosts were reported: *Larix decidua, L. occidentalis, Abies pectinata, Pinus austriaca, P. laricio, P. pumilio* and *P. sylvestris.* Likewise Seymour in his compilation of published fungus records (Host

Index. 1929), listed *Dasyscypha Willkommii* on *Larix laricina* and *L. occidentalis,* and *D. calycina* (Schum. ex Fries) Fuckel on *Pinus rigida, P. sylvestris* and *Abies balsamea. D. Willkommii* (Hartig) was given as a synonym for the species on pine.

The authors who have examined considerable *Dasyscypha* material collected throughout the United States confirm Kauffman's and Weir's observations for they have never observed typical cankers on native larch species, which were associated with large-spored *Dasyscyphae.* The North American forms on *Larix,* which this study has shown to be distinct morphologically and physiologically from the introduced *D. Willkommii* and *D. calycina,* are described as new species:

Dasyscypha oblongospora sp. nov. (PLATE 11, 12).

Apothecia, waxy, fleshy, sparse (PLATE 11, FIG. 1), scattered or grouped erumpent, at first, globular, closed, opening in a roundish form, margin inclosed, urn-like, becoming expanded under moist conditions laterally compressed and closed when dry (PLATE 11, FIGS. 1, 2), shortly but distinctly stipitate; externally whitish or greyish-white, with long, flexuous excipular hairs minutely roughened, hyaline, thin-walled, cylindrical with subacute, gently rounded extremities (PLATE 12, FIG. 3), septated, forming elongated cells, 3–4 μ broad, persistent; disc salmon-orange to orange-buff, 0.5–2 mm. diameter. Asci clavate, apex obtusely rounded, range (200) 68.4–115.2 $\times$ 7.0–10.0 μ; commonly 72–97 $\times$ 7–9 μ (PLATE 12, FIG. 1). Ascospores eight, uniseriate or irregularly and loosely arranged, hyaline, smooth, continuous at first, commonly becoming uniseptate upon germination, distinctly oblong, or oblong-elliptic with obtuse extremities; biguttulate, range (200) 10.0–16.0 $\times$ 3.8–6.0 μ, commonly, 11–15 $\times$ 4–6 μ (PLATE 12, FIG. 2). Paraphyses outranking asci, flexuous, septate, filiform not swollen toward the tip or very slightly so, with obtuse extremities, conspicuously minutely guttulate, (100) 90.0–133.2 $\times$ 1.0–2.0 μ, extremities 1–2.5 μ broad (PLATE 12, FIG. 1).

Conidial stage consisting of waxy, fleshy, erumpent stromata with irregular, labyrinthiform cavities in which the microconidia (spermatia) are abstricted from the tips of slender, subulate, acutely-pointed, simple or verticillately-branched sporophores (PLATE 12, FIG. 4); microconidia hyaline, continuous, elliptic-oblong or allantoid, with obtuse extremities, (100) 2–5 $\times$ 1–1.5 μ (PLATE 12, FIG. 5). Germination not observed.

Ascomatibus sparsis, solitariis vel gregariis, erumpentibus, distincte breviter stipitatis; initio subglobosis, dein cyathiformibus, cupulis humidulis planiusculis; margine in sicco semper connivente; disco carneo-aurantiaco vel luteo-aurantiaco; 0.5–2 mm. diam.; extus albidis vel griseo-albidis, tomentosis; pilis elongatis, hyalinis, septatis, minute asperatis, 3–4 μ crassis. Ascis octosporis, clavatis subcylindraceis, 68.4–115.2 $\times$ 7.0–10.0 μ, vulgo 72–97 $\times$ 7–9 μ. Ascosporis monostichis, continuis, hyalinis, distincte oblongis, vel oblongis-ellipsoideis 10.0–16.0 $\times$ 3.8–6.0 μ, vulgo 11–15 $\times$ 4–6 μ. Paraphysibus filiformibus, septatis, ascos superantibus, apice obtusis vel rarius sursum incrassatulis, guttulatis, 90.0–133.2 $\times$ 1.0–2.0 μ, apice 1.0–2.5 μ crassis.

Fructificationibus conidicis carnosis, ceraceis, erumpentibus, loculiis simplicis vel labyrinthiformibus, basidiis hyalinis, filiformibus, subuliformibus, simplicibus vel verticillate; ramosis, microconidiis (spermatiis) hyalinis, continuis, ellipsoideo-oblongis, vel allantoidiis, (100) 2–5 $\times$ 1–1.5 μ crassis.

Hab. in ramulis emortuis *Laricis laricinae, L. leptolepis, L. europeae, Pini pungentis, P. virginianae, Piceae pungentis, Pseudotsugae taxifoliae* in America boreali. Specimen typicum *53156, L. laricina* in Herb. Myc., U. S. D. A., Washington, D. C.

Habit.—The type specimen, *53156* with a slide of *D. oblongospora* collected on dead branches of *Larix laricina,* Bethel, Vt., by Spaulding, May 8, 1931, have been deposited in the Mycological Herbarium, U. S. D. A., Washington, D. C.

Other specimens of the fungus on Abieteae made 1927–1932 in the collections of the Division of Forest Pathology, have been studied:

On *Larix europaea.* Michigan,—*43552,* Fennville, coll. J. R. Hansbrough; *43568,* Bailey, coll. J. R. H.; *53816,* Forest Plantation, Univ. Michigan, coll. D. V. Baxter. Maine,—*16389,* Lisbon Falls, coll. J. R. H.; *53053,* Lisbon Falls, coll. M. A. McKenzie; *53771,* Lisbon Falls, coll. McK. & K. F. Aldrich. Massachusetts,—*43563,* Hamilton, coll. Hahn; *53175,* Hamilton, coll. McK. & K. F. A.; *53191–2,* Hamilton, coll. Hahn & C. K. Goodling; *53745,* Hamilton, coll. McK.; *53749–69–72–73–74,* Nantucket, K. F. A. & McK. New York,—*43549,* Afton, coll. A. G. Baker; *53001,* So. Millbrook, coll. Baker & R. P. True; *53002,* Fulton, coll. Baker. Pennsylvania,—*53767,* Dimock, Baker & True.

On *Larix laricina.* Michigan,—*43577,* Greenville, coll. Baxter. Vermont,—*53039–42–45–47,* Bethel, coll. P. Spaulding, N. O. Howard & Hahn; *53156,* Bethel, coll. P. S. New Hampshire,—*53074,* Oxford, Cube Mt., C. S. Moses; *53872,* Littleton, J. R. H. Massachusetts,—*16212,* Ipswich, J. R. H.; *53021,* Richmond, Baker; *53044,* Hamilton, N. O. H.; *53720,* Ipswich, McK. & K.

F. A. Connecticut,—*53000,* Sharon, Baker; *53810,* Sharon, J. L. Bedwell. New York,—*16369,* Woodgate, H. Metcalf; *43574,* Boonville, Baker; *53020,* Nundara, Baker, *53023,* Saratoga, Baker; *53024,* Millerton, Baker; *53078,* Loon Lake, Baker. Pennsylvania,—*53759–60–62–63–64–65–93,* Pocono Mts., Baker & True; *53766,* Carbondale, Baker & True; *53768,* Thompson, Baker & True, *53770,* Dimock, Baker & True. Quebec Prov.,—*63198,* Bonaventure, Eno.

On *Larix leptolepis.* Massachusetts,—*43560,* Hamilton, H. Metcalf, P. S., N. O. H. & Hahn; *43598,* Ipswich, coll. N. O. H., J. R. H. & Hahn; *43599,* Hamilton, coll. N. O. H., J. R. H. & Hahn.

On *Picea pungens* Engel. Massachusetts,—*53755,* Hamilton, coll. Ayers; *53839,* Hamilton, coll. Hahn.

On *Pinus pungens* Lam. Pennsylvania,—*53881,* Greenwood Furnace, coll. P. S.

On *P. virginiana* Miller. Pennsylvania,—*16717,* Stone Creek, coll. L. O. Overholts & P. S.

On *Pseudotsuga taxifolia* (blue form). Massachusetts,—*16201,* Hamilton, coll. J. R. H.; *53185,* Hamilton, coll. Goodling & Hahn.

Dasyscypha occidentalis sp. nov. (PLATE 12, 13).

Apothecia waxy, fleshy, abundant (PLATE 13, FIGS. 1, 2, 3), scattered or grouped, erumpent, at first globular, closed, opening in a roundish form, margin inclosed, urn-like, becoming widely expanded, saucer-like under moist conditions (PLATE 13, FIG. 3), laterally compressed and closed when dry; shortly but distinctly stipitate; externally whitish with flexuous, cylindrical hairs minutely roughened, hyaline, thin-walled with blunt, obtuse, gently rounded extremities, septated, forming short cells, 3–4 μ broad, brittle, readily breaking away revealing the glabrous ascocarp beneath (PLATE 12, FIG. 8); disc orange-buff to salmon-orange, 1–3 mm. diameter. Asci clavate, apex obtusely rounded, range (400) $86.4–129.6 \times 6.0–12.0 \mu$, commonly, $94–119 \times 8–10 \mu$ (PLATE 12, FIG. 6). Ascospores eight uniseriate, arranged in a close-set, regular, oblique manner, hyaline, smooth, continuous at first, becoming commonly uniseptate on germination, elliptical, blunt with obtuse extremities, range (380) $10.6–18.0 \times 4.0–7.8 \mu$, commonly, $12–16 \times 5–6 \mu$ (PLATE 12, FIG. 7). Paraphyses outranking asci, flexuous, filiform, septate, distinctly swollen at tips, becoming

spathulate, interspersed with paraphyses unswollen at the tips or just slightly so, (222) 82.8–180.0 × 1.0–2.0 μ, extremities 1–5 μ broad (PLATE 12, FIG. 6).

Conidial stage consisting of a waxy, fleshy, erumpent stromata with irregular labyrinthiform cavities in which the microconidia (spermatia) are abstricted from the tips of slender pointed or simple verticillately branched sporophores (PLATE 12, FIG. 9); microconidia continuous, elliptic-oblong or allantoid with obtuse extremities, (100) 2–5 × 1–1.5 μ (PLATE 12, FIG. 10). Germination not observed.

Ascomatibus confertis, solitariis vel gregariis, erumpentibus, distincte breviter stipitatis, initio subglobosis, dein cyathiformibus, cupulis humidulis expansis; margine in sicco incurvatis; disco carneo-aurantiaco, 1–3 mm. diam.; extus primitus tomentosis, albidis, demum nudis, glabris; pilis, hyalinis, septatis, minute asperatis, 3–4 μ crassis. Ascis octosporis, clavatis, subcylindraceis, 86.4–129.6 × 6.0–12.0, vulgo 94–119 × 8–10 μ. Ascosporis monostichis, continuis, hyalinis, ellipsoideis, ellipsoideo-oblongis vel ovatis, apice obtusis, 10.6–18.0 × 4.0–7.8 μ, vulgo 12–16 × 5–6 μ. Paraphysibus filiformibus, septatis, ascos superantibus, apice obtusis, vulgo distincte sursum incrassatulis, spathulatis, vel raro submoniliformibus; 82.8–180.0 × 1.0–2.0 μ; apice 1–5 μ crassis.

Fructificationibus conidicis carnosis, ceraceis, erumpentibus, loculiis simplicis, vel labyrinthiformibus; basidiis, hyalinis, filiformibus, subuliformibus, simplicibus vel verticillate ramosis; microconidiis (spermatiis) hyalinis, continuis, ellipsoideo-oblongis vel allantoidiis, 2–5 × 1–1.5 μ crassis.

Hab. in ramulis emortuis *Laricis occidentalis*, *L. europaea*, *L. leptolepis*, *L. laricinae* in America boreali. Specimen typicum *40485*, *L. occidentalis*, in Herb. Myc. U. S. D. A., Washington, D. C.

Habit.—The type specimen, *40485*, with a slide of *D. occidentalis*, collected on dead branches of *Larix occidentalis*, Hills, B. C., by J. L. Mielke, June 23, 1928, have been deposited in the Mycological herbarium, U. S. D. A., Washington, D. C.

Other specimens of the fungus on Abieteae, made in 1927–1928 and 1931, in the collections of the Division of Forest Pathology, have been studied:

On *Larix europaea*. Massachusetts,—*53174*, Hamilton, coll. McKenzie & K. F. Aldrich. New York,—*43548*, Woodgate, coll. Baker; *53003*, Warrensburg, coll. Baker.

On *Larix laricina*. Vermont,—*16271*, Bethel, coll. P. Spaulding; *53038–40–157*, Bethel, coll. P. S., N. O. Howard & G. G. Hahn. New York,—*43573*, Utica, coll. Baker; *53022*, Brook, coll. Baker; *53077–86*, road from Johnstown to Ephrata, coll.

Baker & R. P. True. Pennsylvania,—*53770,* Dimock, Baker & True.

On *Larix leptolepis.* Massachusetts,—*53041–073,* Hamilton, coll. Hahn; *53075,* Hamilton, coll. Hahn, T. T. Ayers & C. S. Moses.

On *Larix occidentalis.* Washington,—*52372,* Northport, coll. G. G. Hedgcock. Oregon,—*40693,* Horse Thief Meadows, Mt. Hood, coll. J. R. Hansbrough. Montana,—*16270,* Belton, coll. C. R. Stillinger. British Columbia,—*40473* (dupl. *45825*), Nelson, coll. J. L. Mielke; *40484,* Hunters Siding (Rosebery) coll. J. L. M.; *40485,* Hills, Slocan Lake, coll. J. L. M. & H. G. Lachmund; *40512,* Hunters Siding, coll. J. R. H.; *45824,* Hills, coll. H. G. L.; *53100,* Hunters Siding, coll. J. R. H.; *53101,* Apex (Nelson), coll. J. R. H.

CULTURE NOTES

There is not available space in this article to give in detail all the culture data with respect to the Dasyscypha group herein discussed. In all approximately 2,000 cultures have been studied which have aided greatly in allocating forms. Only the following brief notes will be given at this time. Mono-ascus and mono-ascospore cultures of the *Dasyscypha* species grew slowly but vigorously upon 3 per cent malt agar. In the earlier studies a malt produced in Brunswick, Germany, which had been used with success by Plassmann (**10**), was employed. It was found that culture growth succeeded best at low temperatures and on substrata having a pH value approximately 5.0 to 6.0. The ascospores which germinated in certain instances after nine months' keeping were commonly uniseptate with polar germ tubes. Upon the malt medium the following characteristics were recorded:

Dasyscypha calycina. Germinated ascospores produced an elongate, scantily branched, flexuous type of germination (PLATE 8, FIG. 3) within three days. Strains of the fungus produced a whitish, close-set, low, "mealy," aërial growth (PLATE 8, FIG. 4) over the surface of the slant which showed indistinct zonations and a somewhat ray-like or striated appearance. A dense, white-tufted, cottony growth formed at the apex of the slant and a light pinkish-buff or ochraceous-buff, or cinnamon-buff color formed in the

aërial hyphal stratum. Cultural agreement between American and Scottish cultures was observed. The imperfect stage formed scantily.

D. Willkommii. Germinated ascospore produced a clumped, "mycorrhiza-like" germination consisting of profusely-branched, comparatively short hyphae, pronouncedly sinuous or "curly" in appearance (PLATE 10, FIG. 5). Lohman (Mich. Acad. Sci. **15**: *pl. 11, fig. 4,* 1932) figures a somewhat similar branched, coiling type of germ tube development for *Hysterographium fraxini* (Fries) de Not. Strains of the fungus isolated from cankers in Massachusetts (PLATE 10, FIG. 1) showed extremely little variation and agreed culturally with those isolated in Scotland. A dense, chalky-white, velvety, aërial growth covered the slant with evident zonations (PLATE 10, FIG. 4). Dense, cottony mycelial tufts, some 5 mm. across at the top, formed at the apex of the slant and along the sides of the tubes. A light pinkish-buff or pale ochraceous-buff color appeared in the aërial hyphae which became ochraceous-salmon with age. The imperfect stage formed scantily.

D. oblongspora. Germinated ascospores produced elongate germ tubes which in three days were unbranched or had produced exceedingly few, short lateral branches (PLATE 11, FIG. 3). This species produced the imperfect stage in great abundance. The surface of the slant was covered with a low-growing, whitish, coarse-matted, woolly, indistinctly zonate, aërial growth, somewhat flocculent in appearance in which formed ochraceous-tawny, conidial fruit bodies. With age a light buff color appeared and the conidial exudates became Mars brown. Tufted hyphae were lacking at the apex of the slant (PLATE 11, FIG. 4).

D. occidentalis. Germinated ascospores produced a clumped, branched germination within 3 days, comparable with that produced by *D. Willkommii* except that the hyphae instead of being "curly," were flexuous, tending to be straight (PLATE 13, FIG. 5). The colony was completely covered by a dense, fine, woolly growth, slightly zonate, which became tinged with a light buff color (PLATE 13, FIG. 4). A tawny color appeared in the substratum. The imperfect stage was produced scantily.

On a natural medium consisting of fresh twigs of European larch sterilized with a plug of ground oat agar, the imperfect stage formed more readily with all the species. However, it was very noticeable in the case of *D. oblongospora* that microconidia production was most abundant.

DISCUSSION

The data dealing with the taxonomy and nomenclature of the large-spored *Dasyscypha* forms presented in this paper, will be of value not only to mycologists but pathologists as well. Our problem has been to attempt to say with accuracy what is meant by *Dasyscypha calycina* (Schum.) Fuckel and *D. Willkommii* (Hartig) of the European writers. Heretofore these names have been interpreted so variously that the actual occurrence of these species in North America has been seriously open to question. It is very probable that many of the American collections, heretofore identified as *D. calycina* or *D. Willkommii,* are the two new species herein described, or separate species. This whole matter of nomenclature would be of purely academic interest but for the fact that the host range of the European larch canker parasite involves economically important species.

In Europe it is the general consensus of opinion that the larch canker organism occurs parasitically and saprophytically on a number of coniferous hosts including Douglas fir. At the beginning of this investigation, morphological and physiological differences became evident to the senior author while conducting a preliminary investigation of larch and Douglas fir *Dasyscypha* forms in Scotland in 1929. Culture studies were first made of the saprophytic form on green Douglas fir growing intermixed with badly diseased European larch in a plantation at Glentress, Peeblesshire, Scotland. This *Dasyscypha* with smaller apothecia occurring on the Douglas fir, fruited only sparsely upon the lower suppressed branches, which were dead or dying. Typical *Dasyscypha* cankers, which occurred so abundantly on the larch, were not present on the Douglas fir. Isolations of single ascospores from the Douglas fir *Dasyscypha,* produced a type of germination (PLATE 8, FIG. 3) distinct from that formed by isolations made from the large fruit bodies of *D. Willkommii* taken from active

larch cankers on living tissue (PLATE 10, FIG. 5). The results of this test were repeated several times.

The same phenomenon was sought among germinated ascospores taken from ascocarps produced on the active canker itself and from smaller fruit bodies produced upon dying and dead larch trees, and upon fallen branches. Isolations of ascospores from this smaller form produced a type of germination (PLATE 8, FIG. 3) identical with that produced by the *Dasyscypha* form on Douglas fir. Cultures from this source (PLATE 8, FIG. 4) proved to be distinctly different from those of *D. Willkommii* (PLATE 10, FIG. 4).

These two forms were observed fruiting upon the same cankers on small living branches of the European larch. One of these which appeared to be the parasite, produced abundantly, large. robust apothecia (PLATE 10, FIGS. 2, 3), whereas the other (PLATE 8, FIG. 2), confined to the tissue weakened by the girdling action of the canker, fruited sparsely. Later, however, after the death of the branch part had occurred, this secondary form produced abundant apothecia. Isolations from these two forms produced the distinct types of germination and culture characteristics alluded to above. The secondary or saprophytic form was later determined as *D. calycina*.

Subsequent isolation studies of the introduced larch canker organism in the United States, have shown the same culture characters as those previously observed in Scotland. This can also be said for the European saprophytic species, *D. calycina*, which was probably introduced into New England simultaneously with *D. Willkommii;* for it has only been found in the area where *D. Willkommii* was introduced.

It is the opinion of the writers that the European larch canker parasite does not occur on hosts other than those belonging to the genus *Larix*, and always in close association with the lesions produced by the fungus. When the part attacked has been killed or weakened, secondary saprophytic forms come in. Artificial inoculation studies have shown that whereas *D. Willkommii* will infect larch species, the organism will not grow upon inoculated weakened larch, dead or dying, or upon living or weakened Douglas fir (blue form). The native *Dasyscyphae* described in this

paper are known only as saprophytes, and *D. calycina* is regarded likewise. *D. calycina* would not infect healthy inoculated larch or Douglas fir, but when inoculated into plants of the latter host, which were dying, the fungus produced fruiting bodies.

Since *D. Willkommii* has been found only on species of larch, Plassmann (**11**) is quite correct in his opinion that this fungus is not to be feared as a new enemy of Douglas fir. However, it is the author's belief that Plassmann was concerned with *D. calycina,* or a nearly related form, when he confirmed Day (Empire For. Jour. **7**: 112–115, 1928) in his determination of British material of the European larch canker parasite on *Pinus sylvestris* and *Pseudotsuga taxifolia* (green form). Although it must be admitted that Plassmann questioned the parasitism of the organism on Douglas fir, he tended to regard *D. Willkommii* as a saprophyte on that host in Britain.

The two types of germination discussed for *D. Willkommii* and *D. calycina* are distinctly different from those of the native forms. Because the latter differ morphologically as well as physiologically they are tentatively regarded as new species. Because of the close natural relationships between the species of this group, segregation proved somewhat difficult, *i.e.,* the separation of *D. calycina* and *D. occidentalis.* Nevertheless the authors regard these two physiologically distinct forms as separate species, not only because of the larger size of the asci and spores of *D. calycina* but also because of the submoniliform type of paraphyses (PLATE 9, FIG. 6) produced commonly by the fungus. The latter structures while not entirely lacking in *D. occidentalis* are replaced in the new species by filiform paraphyses characteristically more or less swollen at the tips (PLATE 12, FIG. 6). Further differentiation among the large-spore forms was sought in a comparison of the imperfect stages, but sufficient difference was not found.

Because of the close agreement between cultures of *D. Willkommii,* the authors regard this as a homogenous species. They consider the production of large apothecia and large ascospores as an inherent character, rather than the result of the growth of the fungus on different substrata. On the other hand, Hiley (**6**, p. 79) and other European workers concluded that the European larch canker organism was a heterogenous species, comprised of

a number of intermediate forms between the parasitic and saprophytic types. In Europe, as in America, a number of closely related forms may be present which can be differentiated only by an intensive morphological and physiological study.

SUMMARY

With the discovery in 1927 of the European larch canker disease in Massachusetts, a study has been made of the organisms associated with the canker in order to determine their relationships. The identification of the causal fungus and its distribution in the United States became a problem of considerable importance because of the economic host species involved; for in Europe the European larch canker organism has been reported on the valuable Douglas fir and other conifers. Furthermore fungi purported to be the European larch canker parasite were recorded as being present in North America, before the actual discovery of the disease in this country.

The organism which has been demonstrated as causing European larch canker, should be called *Dasyscypha Willkommii* (Hartig) Rehm, and not *D. calycina* (Schum.) Fuckel. The introduced parasite (*D. Willkommii*) was identified on imported *Larix europaea* and *L. leptolepis* in two localities in Massachusetts. The organism was always found in close association with the cankers which it produced on living tissue. Although the blue form of Douglas fir (*Pseudotsuga taxifolia*) was growing in close proximity to the diseased *Larix europaea,* it did not become infected with the European larch canker disease. Artificial infection with *D. Willkommii* succeeded on young trees of species of larch, but they were unsuccessful not only on dead or dying tissue of the same host, but also upon healthy and dying Douglas fir (blue form).

Dasyscypha calycina Fuckel (nec *Peziza calycina* Schum.), as has been pointed out in this paper, is distinct morphologically and physiologically from *D. Willkommii,* and should be recognized as separate species. It should not be confused with the pre-Friesian species, *P. calycina* Schum. or with *P. calycina* Fr. An amended description is given.

D. calycina which is regarded as a saprophyte, is believed to have been introduced into this country with the European larch canker parasite, for it has only been collected in the area where the European disease was discovered. *D. calycina* was collected on *Larix europaea, L. leptolepis* and *Pseudotsuga taxifolia.* Artificial inoculations with *D. calycina* on living larch and Douglas fir (blue form) did not succeed. The fungus was able, however, to produce fruiting bodies on the same form of Douglas fir which was dying at the time of inoculation, thereby showing its saprophytic nature.

Both *D. Willkommii* and *D. calycina* are distinct morphologically and physiologically from nearly related, large-spore, native forms occurring on larch and other coniferous species. These forms, which heretofore have been identified as *D. Willkommii* or *D. calycina,* are described (p. 88, 90) as new species: *D. oblongospora* Hahn and Ayers, collected on *Larix laricina, L. europaea, L. leptolepis, Pseudotsuga taxifolia,* blue form, *Picea pungens, Pinus pungens* and *P. virginiana; D. occidentalis* Hahn and Ayers, collected on *L. occidentalis, L. laricina* and *L. leptolepis.* These native organisms, the present known geographical range of which is given, do not cause canker on larch or Douglas fir.

Grateful acknowledgment is due Dr. Perley Spaulding, Division of Forest Pathology, for rendering every possible assistance in obtaining *Dasyscypha* material for study and the opportunity of using his extensive bibliography file; and to Dr. W. W. Diehl, Division Mycology, Bureau of Plant Industry, for valuable information with regard to herbarium specimens and advice with respect to matters of nomenclature and taxonomy. The writers would also tender thanks to the following who have kindly loaned or given information concerning specimens: Director R. Chodat, Herbier Boissier, Geneva; Prof. Dr. K. von Tubeuf, Botanisches Institut, Munich; Prof. Dr. E. Ulbrich, Botanisches Museum, Universität Berlin; Dr. Eberhard Plassmann, Forstlichen Hochschule, Hann-Münden; Director A. W. Hill and Miss E. M. Wakefield, Royal Botanic Gardens, Kew; Dr. Malcolm Wilson, University of Edinburgh, Royal Botanic Garden; the late Mr. A. B. Seymour, the officials of Farlow Herbarium, Harvard University and Dr.

C. W. Dodge, formerly of that institution; the Director and Dr. F. J. Seaver of The N. Y. Botanical Garden. We are also grateful to Dr. G. D. Darker for fresh European material and to Mr. J. R. Hansbrough, Division of Forest Pathology, not only for assistance in the early Dasyscypha culture study but also for numerous collections that were augmented by various workers in the same Division. We are indebted to Mr. M. L. F. Foubert for a number of the photographs of the Dasyscypha habit studies.

DIVISION OF FOREST PATHOLOGY, BUREAU OF PLANT INDUSTRY,
IN COÖPERATION WITH THE OSBORN BOTANICAL LABORATORY,
YALE UNIVERSITY, NEW HAVEN, CONN.

EXPLANATION OF PLATES

PLATE 8

Dasyscypha calycina Fuckel (nec *Peziza calycina* Schum.).

Fig. 1. Type Fungi Rhen. *1206,* Herb. Fuckel, Herbier Boissier, Institut Botanique, Geneva. The figure shows only a portion of the entire specimen photographed. Approx. × 6.

Fig. 2. Habit, on *Larix europaea.* Approx. × 11.5

Fig. 3. Ascospore on surface of malt agar, three days after germination. × 300.

Fig. 4. Two four-months-old mono-ascospore malt agar cultures isolated from a single ascocarp, coll. *43564,* saprophytic, *Larix europaea,* Hamilton, Mass. Note: "mealy" aërial growth. Nat. size.

PLATE 9

All drawings made with camera lucida, × 750. Those of the imperfect stage were made from material procured in mono-ascospore culture.

Dasyscypha Willkommii (Hartig) Rehm.

Fig. 1. Asci and paraphyses.
Fig. 2. Ascospores.
Fig. 3. Excipular hairs.
Fig. 4. Sporophores.
Fig. 5. Microconidia.

Dasyscypha calycina Fuckel.

Fig. 6. Asci and paraphyses.
Fig. 7. Ascospores.
Fig. 8. Excipular hairs.
Fig. 9. Sporophores.
Fig. 10. Microconidia.

PLATE 10

Dasyscypha Willkommii (Hartig) Rehm.

Fig. 1. Typical European larch canker on *Larix europaea,* Hamilton, Mass., showing apothecia fruiting on lesion of branch killed by the fungus. Approx. nat. size.

Fig. 2. Apothecia not fully expanded. Note: heavy chalky-white rim. Approx. × 11½.

Fig. 3. Apothecia showing the robust convolute margin. Under moist conditions this may split in a cruciform manner. Approx. × 11½.

Fig. 4. Two three-months-old monoascospore cultures on malt agar, isolated from a single ascocarp, coll. *43559*, Hamilton, Mass., from a canker on a living branch of *Larix europaea.* Note: dense white, velvety aërial growth. Nat. size.

Fig. 5. Ascospore three days after germination on malt agar. Note: "curly" or "mycorrhizal" type of mycelial growth. × 300.

PLATE 11

Dasyscypha oblongospora Hahn & Ayers.

Fig. 1. Habit, on *Larix europaea,* material, coll. *53053,* Lisbon Falls, Maine. Approx. × 11½.

Fig. 2. Apothecia on *Picea pungens,* scant material. Culturally the spruce form agreed with the strains isolated from larch. Approx. × 11½.

Fig. 3. Ascospore from material collected on *Larix laricina,* Bethel, Vt., three days after germination on malt agar. × 300.

Fig. 4. Two two-and-one-half-months-old mono-ascus cultures on malt agar. Isolations were made from a single ascocarp, coll. *43560,* dead twigs of *Larix europaea.* Nat. size.

PLATE 12

All drawings made with the camera lucida × 750. Those of the imperfect stage were made from material procured in mono-ascospore culture.

Dasyscypha oblongospora Hahn & Ayers.

Fig. 1. Asci and paraphyses.
Fig. 2. Ascospores.
Fig. 3. Excipular hairs.
Fig. 4. Sporophores.
Fig. 5. Microconidia.

Dasyscypha occidentalis Hahn & Ayers.

Fig. 6. Asci and paraphyses.
Fig. 7. Ascospores.
Fig. 8. Excipular hairs.
Fig. 9. Sporophores.
Fig. 10. Microconidia.

PLATE 13

Dasyscypha occidentalis Hahn & Ayers.

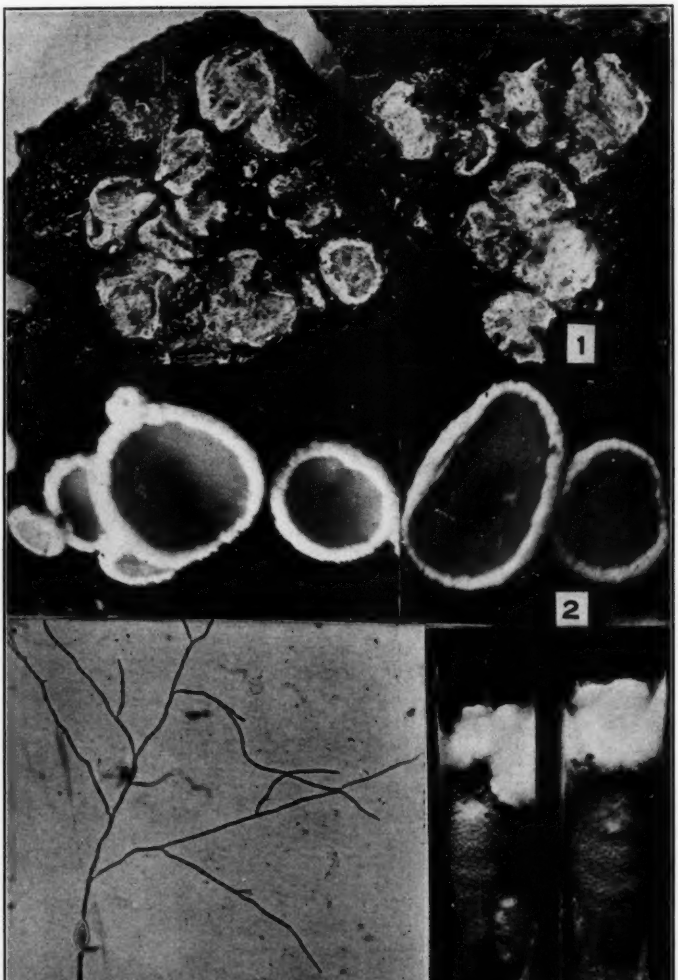
Fig. 1. Apothecia, British Columbia material, coll. *40512,* Hunters Siding, Rosebery, saprophytic on dead twigs, *Larix occidentalis.* Approx. × 11½.

Fig. 2. Habit, Bethel, Vt., material, coll. *53038,* saprophytic on *L. laricina.* Approx. × 4.

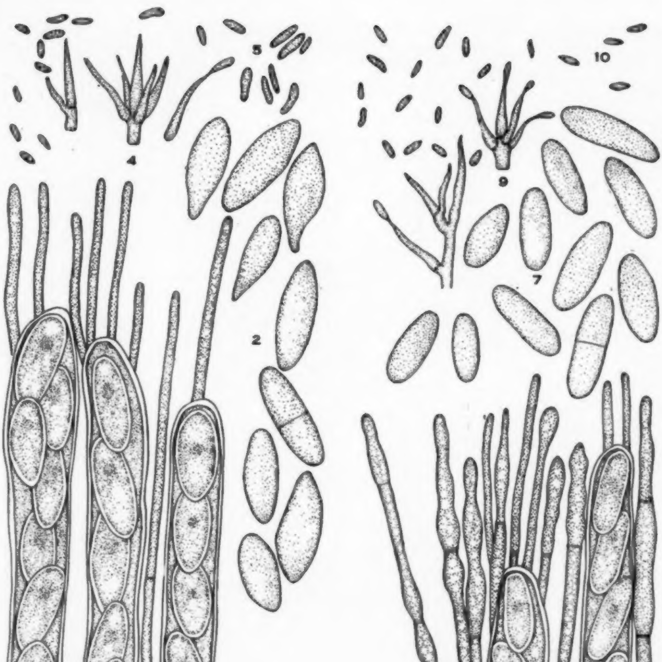
Fig. 3. Habit, Hamilton, Mass., material, coll. *53087,* saprophytic on *L. leptolepis.* Cups moist and expanded. Approx. × 4.

Fig. 4. Three two-months-old mono-ascospore cultures on malt agar; one on left from *L. occidentalis,* B.C., two on right from *L. laricina,* N. Y. Note: dense aerial growth covering entire colony. Nat. size.

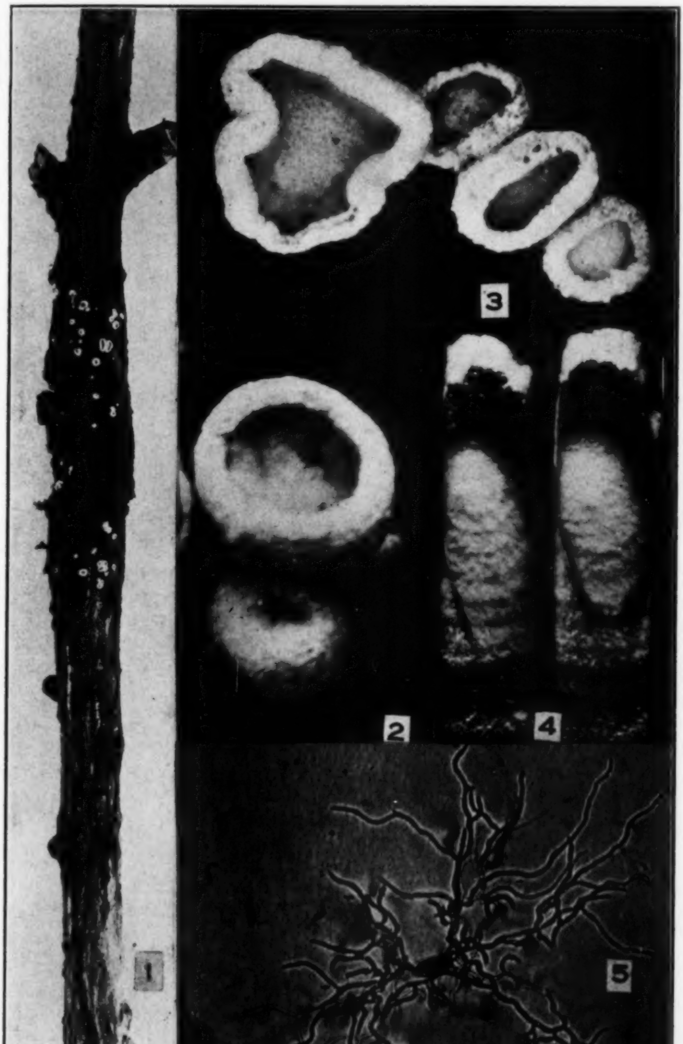
Fig. 5. Germinated ascospore (N. Y. material) four days old on malt agar. Note: clumped type of growth but not "curly" as in the case of *D. Willkommii.* × 300.



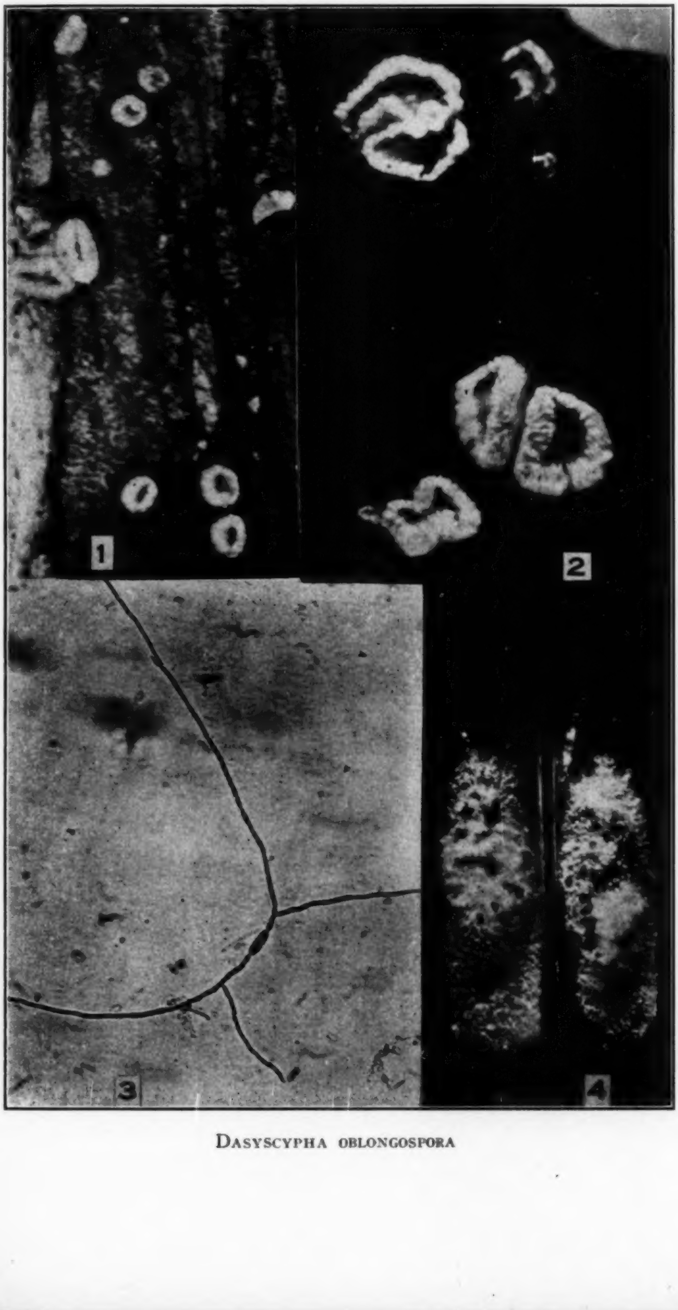
DASYSCYPHA CALYCINA



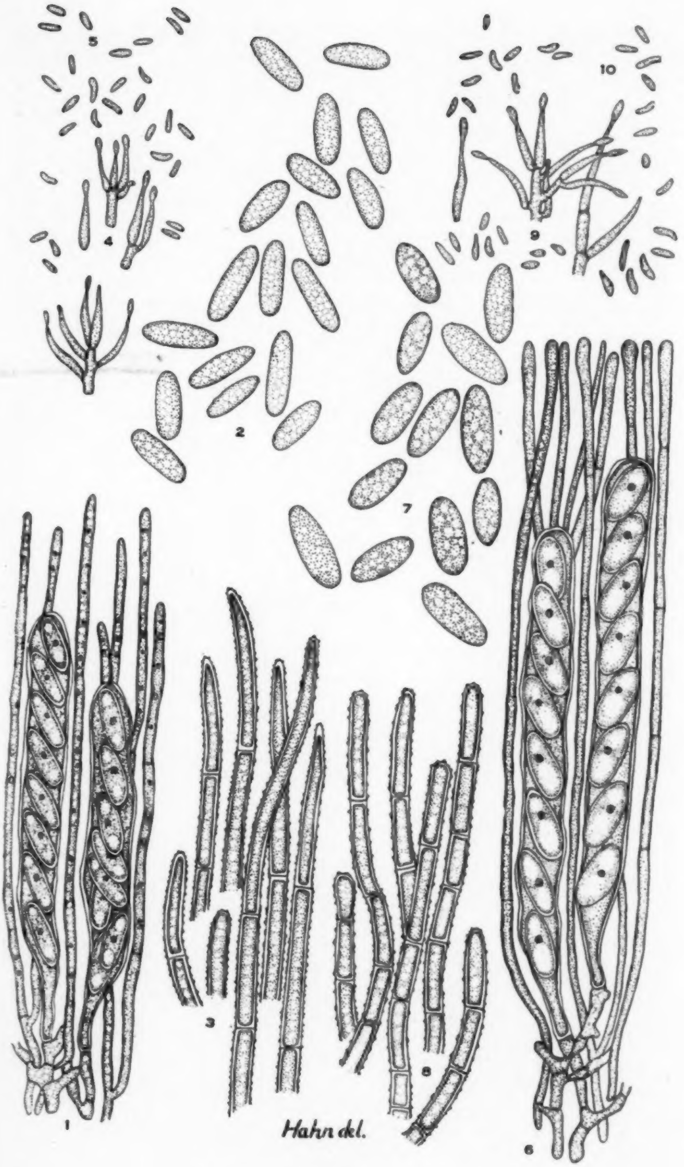
1–5 DASYSCYPHA WILLKOMMII
6–10 DASYSCYPHA CALYCINA



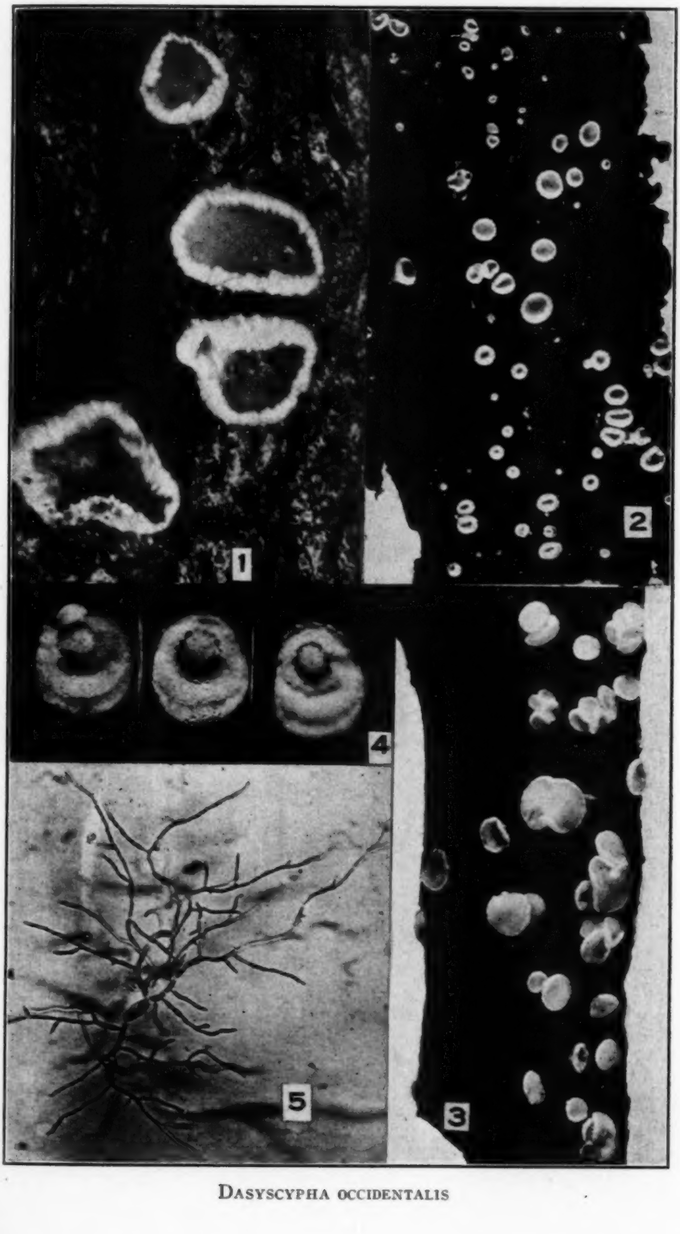
Dasyscypha willkommii



Dasyscypha oblongospora



1–5 DASYSCYPHA OBLONGATA
6–10 DASYSCYPHA OCCIDENTALIS



DASYSCYPHA OCCIDENTALIS

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PHOTOGRAPHS AND DESCRIPTIONS OF CUP-FUNGI—XX. A NEW LAMPROSPORA

FRED J. SEAVER

(WITH PLATE 14)

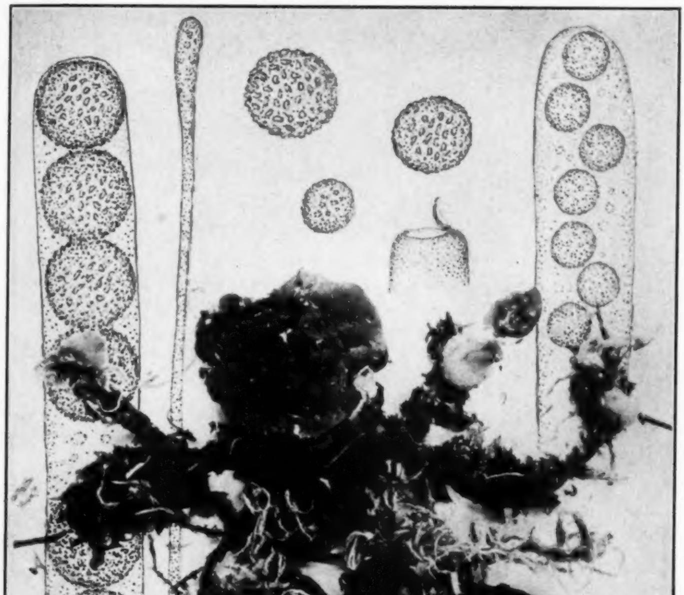
During the summer of 1932 the writer received a collection of cup-fungi growing on *Sphagnum* which had probably been sterilized. Examination at once revealed the fact that it was a species of *Lamprospora* of unusually large dimensions. The spores of this species are quite similar to those of *Lamprospora trachycarpa* but the apothecial characters are entirely different.

Several young apothecia were present and consisted of a globose solid ball reaching nearly a centimeter in diameter and partially surrounded by the leaves and stems of *Sphagnum* on which it was growing. As the apothecia mature the hymenium gradually expands in an irregular manner giving rise to a much convoluted surface. The entire growth is at first whitish later assuming a lavender tint. The one mature apothecium reached a diameter of 3 centimeters.

This species is so different from any which the writer has examined in his studies on this group that he feels compelled to describe it as new. The technical description is as follows:

Lamprospora sphagnicola sp. nov.

Apothecia sessile at first globose and solid, reaching a diameter of 1 cm., gradually expanding and becoming subdiscoid finally reaching a diameter of 3 cm., externally whitish; hymenium strongly convoluted, at first light colored gradually assuming a lavender tint; asci cylindric or subcylindric, tapering into a rather abrupt stem-like base, 8-spored, reaching a length of 215 μ and a diameter of 15 μ; spores at first irregularly disposed, finally becoming definitely 1-seriate, hyaline or subhyaline, at first smooth, soon becoming sculptured reaching a diameter of 12 to 15 μ; spore-sculpturing taking the form of tubercles or very short elongated ridges; paraphyses filiform rather strongly enlarged above reaching a diameter of 4 to 5 μ.



Lamprospora sphagnicola

Apothecia sessilia, primum globosa dein expansa, maturitate hymenio convoluto; ascis cylindraceis v. subcylindraceis, 200 μ long. et 12–15 μ diam.; sporis globosis, primum levibus dein tuberculatis, 12–15 μ diam.; paraphysibus clavatis, apice 15–15 μ diam.

On *Sphagnum* moss, in storage.

Type locality: Experiment Station, Georgia.

THE NEW YORK BOTANICAL GARDEN

EXPLANATION OF PLATE 14

Center, Photograph of one mature apothecium and several young ones showing habitat; Below, Drawing of one immature apothecium enlarged; Right, Drawing of an ascus when immature; Left, Immature ascus with spores and paraphyses; Above, Three stages in the development of the spore; also trip of ascus showing operculum.

Drawings made with the aid of the camera lucida using a 1 inch eyepiece and a 1/8 objective.

PENICILLIUM GLAUCUM OF BREFELD (CARPENTELES OF LANGERON) REFOUND

C. L. SHEAR

(WITH 3 TEXT FIGURES)

The fungus described by Brefeld as *Penicillium glaucum* Link with its perithecial form has so far as we are aware not been reported since. In a collection of cultures of soil fungi isolated from soils at Tela, Honduras, by Dr. Otto A. Reinking, 1931, were several species of *Penicillium,* some producing perithecia. One of these was especially interesting (culture No. 2). It was isolated from soil at various depths from the surface to 10 inches, and said to be fairly common. Sub-cultures in tubes of cornmeal agar produced a very thin white superficial growth, and after a day or two an abundance of pale green conidia of *Penicillium.* A few weeks later numerous globose, pale yellowish perithecia appeared. Various sub-cultures were made from ascospores and conidia. These also produced the same *Penicillium* and the same perithecia and ascospores. Cultures were sent to Dr. B. O. Dodge who also verified the connection between the conidia and perithecia, as did Dr. Charles Thom, of the Bureau of Chemistry and Soils. Careful comparison of these cultures with Brefeld's [1] description and plates shows that they agree with his material, so far as it relates to certain of his plates and figures of conidia and perithecia. It is evident, as has been pointed out by others, that some of Brefeld's cultures were mixed, as more than one species of *Penicillium* is described and illustrated. Our cultures, however agree, so far as the conidial stage is concerned, with his plate 8, figure 51, which also shows the conidia arising from the typical germinating ascospores. For purposes of comparison they are reproduced here (FIG. 1). The perithecial form agrees in practically every detail of development with that so fully described by Brefeld, l. c., and

[1] Brefeld, O. Botanische Untersuchunge über Schimmelpilze. II. Die Entwicklungsgeschichte von Penicillium. 1–98, 1874.

illustrated in his plate 6, figures 34–39, with the exception of the statement that the asci are borne in chains (FIG. 2). This is very difficult to demonstrate, but our observations indicate that the asci are borne on very short branches of ascogenous hyphae as described by Dodge[2] for *P. brefeldianum* and form such a dense mass that they have the appearance of being in chains, though Dodge found one or two cases which showed two or three asci in a chain. The development of the perithecium from a sclerotoid

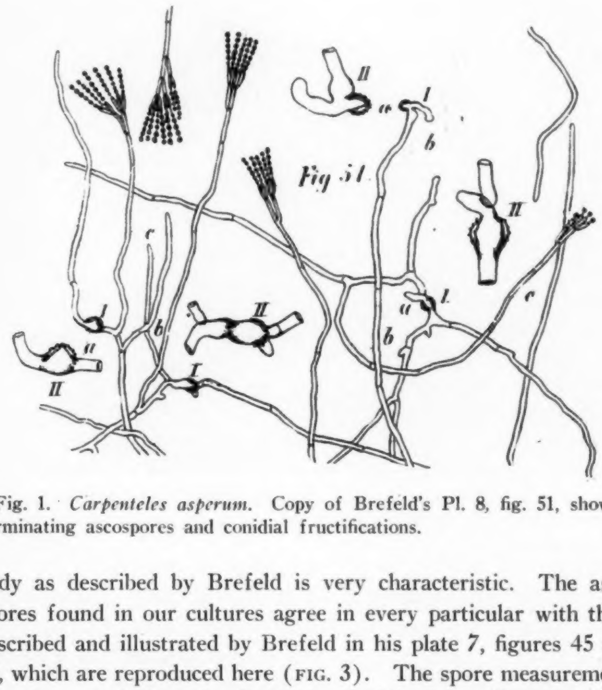


Fig. 1. *Carpenteles asperum.* Copy of Brefeld's Pl. 8, fig. 51, showing germinating ascospores and conidial fructifications.

body as described by Brefeld is very characteristic. The ascospores found in our cultures agree in every particular with those described and illustrated by Brefeld in his plate 7, figures 45 and 46, which are reproduced here (FIG. 3). The spore measurements are given as follows by Brefeld: Conidia 2.5 μ diameter, ascospores $4\text{–}6 \times 4\text{–}4\frac{1}{2}\ \mu$. According to our measurements, the conidia are 2 μ in diameter and ascospores $3\text{–}4 \times 2\text{–}2\frac{1}{2}\ \mu$. This discrepancy in measurements is, however, easily explained by the

[2] Dodge, B. O. The perithecium and ascus of Penicillium. Mycologia **25**: 90–104, 1933.

discovery of Neuhoff[3] that Brefeld's measurements are always too large, due to an error in the scale he used.

The question now arises as to what name this fungus should bear. Brefeld regarded his fungus as *P. glaucum* of Link. It is now generally agreed that it is impossible to tell with certainty to what particular form of Penicillium Link originally applied this name. It is highly improbable, however, that he had the fungus discussed here.

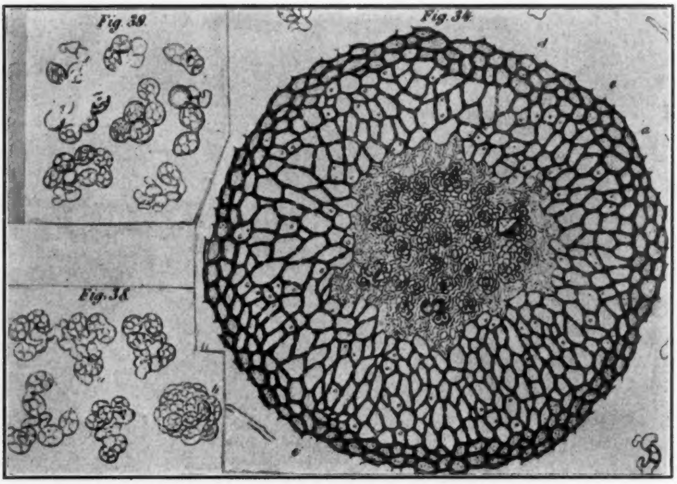


Fig. 2. *Carpenteles asperum.* Copy of Brefeld's Pl. 6, figs. 34–39, showing section of young perithecium and asci and ascospores in different stages of development.

According to the present rules of nomenclature, an ascogenous fungus should bear the generic name applied to its perfect stage. In 1922, Langeron[4] proposed the name *Carpenteles* for species of Penicillium which are known to produce asci and specified as the type of the genus "*P. glaucum* (Link) Brefeld." Langeron, however, did not see the fungus nor verify the connection between

[3] Neuhoff, W. Bot. Archiv. **8**: 253, 1924.

[4] Langeron, Maurice. Utilité de deux nouvelles coupures génériques dans les *Périsporiacés*: *Diplostephanus* N. G. et *Carpenteles* N. G. Comp. Rend. Soc. Biol. Par **87**: 343, 1922.

the conidia and perithecia described by Brefeld and therefore his name has not been adopted by Thom and others. Langeron did not actually publish the combination *Carpenteles glaucum*, but this combination was used by Clements and Shear.[5] In view of the uncertainty regarding the application of *P. glaucum* and the confusion which already exists in its use, it seems best to use another specific name for this ascogenous fungus. We therefore propose the name **Carpenteles asperum** nom. nov., the specific name referring to the spinulose ascospores.

There are several other species of Penicillium which have been shown to have perithecia and spores of the same generic character.

Fig. 3. *Carpenteles asperum.* Copy of Brefeld's Pl. 7, figs. 45 and 46, showing typical ascospores, some of the spores germinating.

Penicillium brefeldianum and its perithecial form described by Dodge, in the paper already cited, is evidently congeneric with *Carpenteles asperum* and should become **Carpenteles brefeldianum** (Dodge) comb. nov. *P. javanicum* van Beijma[6] also belongs here as shown by the studies of Dodge, l. c., which we have verified, and should be **Carpeneteles javanicum** (Van Beijma) comb. nov.

The exact limitations of this genus can not be drawn until the life histories of more of the related species are known. It is clearly related to *Eurotium* which is at present restricted to perithecial forms of *Aspergillus.*

BUREAU OF PLANT INDUSTRY,
WASHINGTON, D. C.

[5] Clements, F. E. & Shear, C. L. The genera of fungi, 297, 1931.

[6] Van Beijma Thoe Kingma, F. H. Mykologische Untersuchungen—*Penicillium javanicum* nov. spec. Ver. Kon. Akad. Wet. Amsterdam **26**: 16–19, 1929.

NOTES AND BRIEF ARTICLES

Bartholomew's Handbook

A serviceable compilation of the rusts of North America has been issued recently by Elam Bartholomew, as a "Handbook of the North American Uredinales." In the 238 pages are enumerated all the species in the 7th volume of the N. Amer. Flora, with 12 additional subtropical species. There are 25 new combinations made, and two new names proposed, *Puccinia longipedicellata* and *P. parnassiaecola*. The generic names *Puccinia* and *Uromyces* are restored. Species are arranged alphabetically under each genus with full synonymy, and with page references to the N. Am. Flora, where descriptions are to be looked for. This second edition is an exact reprint of the 1928 edition, to which has been added a complete index of 52 pages. Beside the index this edition adds the two new names already mentioned, two other subtropical species, and in a supplement reference is made to the species of Milesia recently published by Faull, 12 new species in No. 1–2, vol. 31, of Annales Mycologici, and *Uredo Chardoni* Kern. The work is the only complete list of North American rusts and will be found serviceable to collectors and others in a number of ways and especially to those whose herbarium is arranged on the card index plan.

J. C. Arthur.

The Mycological Society of America

The Council of the Society voted at the Atlantic City meeting that the names of the charter members be published in Mycologia. The Constitution states that the charter members are those who joined before or during the formal organization of the Society at Atlantic City. The contract with the New York Botanical Garden, accepted by the Society December 28, 1932, provided that all personal subscribers then receiving Mycologia might become members of the Society if they so desired. The Council ruled that

those expressing the desire to join should be regarded as charter members. The following list, based on these rulings, contains the names of charter members only.

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Meinecke, E. P.
Miles, L. E.
Miller, Joseph A.
Miller, Julian H.
Miller, L. W.
Miller, Pierre A.
Miura, Mitsushiga
Mix, A. J.
Moffatt, Will S.
Morrow, Marie B.
Morse, Elizabeth E.
Moss, E. H.
Mounce, Irene
Mrak, Emil M.
Müller, Albert S.
Murrill, William A.
Muskatblit, Emanuel
Noguti, Rokuya
Norton, J. B. S.
Nusslé, Helene A.
Orton, C. R.
Overholt, William W.
Overholts, Lee O.
Parish, Jessie A.
Parker, Charles S.
Parks, Harold E.
Persons, T. D.
Petzke, Ernest A.
Plunkett, Orda A.
Pomerleau, René
Poole, R. F.
Porter, C. L.
Pound, Roscoe
Rands, R. D.
Raper, Kenneth
Rice, Mabel A.
Richards, B. L.
Roberts, John W.
Rossett, Joshua
Rudolph, Bert A.
Ruehle, Geo. D.
Rusby, H. H.
Rusden, Philip L.
Sass, John E.
Satin, Sophie
Sawyer, William H., Jr.
Seaver, Fred J.
Setchell, W. A.
Shear, Cornelius L.
Sherbakoff, C. D.
Shimek, B.
Shope, Paul F.
Sinden, James W.
Smart, Robert F.
Smith, Alexander H.
Snell, Walter H.
Solheim, W. G.
Sparrow, F. K., Jr.
Stakman, E. C.
Stevens, Neil E.
Stevenson, John A.
Stewart, Dewey
Stewart, Fred C.
Stifler, Mrs. Cloyd B.
Stout, Gilbert L.
Strong, Miriam C.
Sturgis, Wm. C.
Styer, J. Franklin
Sumstine, David R.
Swartz, Delbert
Swift, Marjorie
Takasugi, Hideo
Taubenhaus, J. J.
Tehon, Leo R.
Thom, Charles
Thomas, William S.
Thompson, G. E.
Thorold, C. A.
Thurston, H. W., Jr.
Togashi, Kogo
Truscott, J. H. L.
Tucker, C. M.
Tullis, E. C.
Utter, L. Gordon
Van Hook, J. M.

Van Horne, Miss A.
Velazquez, Miss Josepha
Voorhees, R. K.
Waksman, Selman A.
Walker, A. R.
Walker, Leva B.
Weber, George F.
Wehmeyer, Lewis E.
Welch, D. S.
Wellman, F. L.
West, Erdman
Westcott, Cynthia
Weston, Wm. H., Jr.
Whetzel, H. H.
White, Richard P.
Wilson, O. T.
Wolf, Frederick A.
Woolliams, G. E.
Young, Paul A.
Yamada, Gentaro
Zeller, S. M.
Zundel, George L.
Zwick, Karl G.